NEKTON USE OF SUBMERGED AQUATIC VEGETATION, MARSH, AND SHALLOW UNVEGETATED BOTTOM IN A LOUISIANA TIDAL FRESHWATER ECOSYSTEM

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OVERVIEW

A large body of research has documented the importance of shallow estuarine habitats to nekton (fishes and decapod crustaceans). Some studies have focused on a single habitat such as seagrass (Adams 1976) or tidal creeks (Cain and Dean 1976). Others have compared the relative value of different habitats to nekton (Zimmerman and Minello 1984; Sogard and Able 1991). Most habitat comparison studies have compared seagrass and unvegetated areas (see reviews by Orth et al. 1984 and Pollard 1984). A few such studies have compared marsh and unvegetated habitats (Zimmerman and Minello 1984; Minello et al. 1991, 1994). The vast majority of these habitat comparison studies have reported higher densities of nekton in seagrass and marsh than over unvegetated bottom (Heck and Thoman 1984; Zimmerman and Minello 1984; Orth and van Montfrans 1987; Heck et al. 1989; Lubbers et al. 1990; Williams et al. 1990; Ferrell and Bell 1991; Sogard and Able 1991; Connolly 1994a; Heck et al. 1995; West and King 1996). Thus, the importance of seagrass and marsh habitats to nekton, especially as nurseries for fishery species, has been well documented (Thayer et al. 1978; Weinstein 1979; Boesch and Turner 1984; Bell and Pollard 1989).

Although less common, similar interhabitat comparisons in tidal freshwater systems have documented the importance of submerged aquatic vegetation (SAV) and emergent marsh vegetation to nekton on the Atlantic coast (McIvor and Odum 1986; Rozas and Odum 1987a, 1987b, 1987c; McIvor and Odum 1988; Rozas et al. 1988). However, studies of habitat use by nekton of tidal freshwater systems on the Gulf coast have not included vegetated habitats and have been restricted to sampling unvegetated bottom using trawls and seines (Juneau 1975; Hoese 1976; Thompson and Deegan 1983; and see review by McIvor and Rozas 1996).

Although marsh, SAV, and unvegetated bottom often co-occur in estuaries, studies comparing the relative value of all three major habitats are few and have not been conducted in tidal freshwater systems (Thomas et al. 1990; Heck et al. 1994; Rozas and Minello 1998). In two habitat-comparison studies restricted to a single species, higher densities of blue crab

Callinectes sapidus were found in vegetated habitats than on unvegetated bottom (Thomas et al. 1990; Heck et al. 1994). Blue crab apparently selected SAV (seagrass) over marsh in most months of one study (Thomas et al. 1990). In a study that included the entire nekton assemblage, Rozas and Minello (1998) found that most species showed an apparent preference for vegetated over unvegetated habitat. Nekton densities in their study were similar in saltmarsh and seagrass; where there were differences, most nekton species apparently preferred saltmarsh habitat. Interhabitat studies of tidal freshwater systems thus far have only compared SAV and unvegetated habitat (Rozas and Odum 1987a) or tidal creeks and marsh surface (Rozas et al. 1988). Consistent with similar investigations, nekton was more abundant in SAV beds than over unvegetated bottom in a tidal freshwater system on the Atlantic coast (Rozas and Odum 1987a).

One of the hypotheses postulated to explain higher nekton densities in (and greater habitat value of) vegetated areas over unvegetated bottom is that vegetated habitat provides more food than unvegetated areas. Higher densities of invertebrates (fish prey) are found in vegetated habitats than on unvegetated bottom (Gerking 1962; Menzie 1980; Lubbers et al. 1990). Experimental enclosure studies have documented that shallow, vegetated habitats provide more food for nekton than deeper, unvegetated habitats (McIvor and Odum 1988; Rozas and Odum 1988). Fish caught in vegetated habitats of estuaries have fuller guts than those in unvegetated habitats (Lubbers et al. 1990), and many fish predators are dependent on the prey contained in vegetated habitats (Huh and Kitting 1985; Whitfield 1988). It seems logical then that fish predators would have more opportunity to consume prey if they inhabited areas where their prey was most abundant. In fact, higher densities of fish predators are often found in habitats that support higher densities of their prey (Lubbers et al. 1990). Therefore, prey abundance and foraging profitability may be factors contributing to apparent habitat selection by nekton.

My study was designed to compare the relative importance of SAV, marsh, and unvegetated habitat to nekton in a tidal freshwater system on the Louisiana coast. In addition,

the study also addressed the following question: are nekton distributions influenced by differences in prey abundance and predator feeding rates among habitats? In chapter 1, I describe a study in which I compare the distribution of nekton among major shallow water habitats and document the composition, relative abundance, and seasonal abundance of nekton in these habitats. I discuss possible causes for the distribution of nekton in my study area and evaluate the relative value of these habitats to nekton, especially as nurseries for some species. I describe a study in Chapter 2 in which I used foraging experiments and sampled prey organisms to compare the potential and actual foraging success of small fish predators in SAV, marsh, and on unvegetated bottom. In Chapter 2, I also discuss how prey availability may influence the distribution of nekton among habitats in the Atchafalaya River Delta. The final section is a brief summary of the conclusions I draw from my research.

CHAPTER 1

INTRODUCTION

Studies of tidal freshwater marshes on the southeast Atlantic coast have shown that submerged aquatic vegetation (SAV) and emergent marsh are important habitats for fish and decapod crustaceans (McIvor and Odum 1986; Rozas and Odum 1987a, 1987b, 1987c; McIvor and Odum 1988; Rozas et al. 1988). However, no such studies of direct use of vegetated habitats by nekton have been conducted in tidal freshwater systems on the Gulf of Mexico coast (see review by McIvor and Rozas 1996); studies of tidal freshwater environments on the Gulf coast have been restricted to sampling unvegetated bottom using trawls and seines (Juneau 1975; Hoese 1976; Thompson and Deegan 1983).

Studies comparing the relative habitat value of emergent vegetation, SAV, and unvegetated bottom in shallow water are few and have excluded the tidal freshwater regions of estuaries (Thomas et al. 1990; Heck et al. 1994; Rozas and Minello 1998). Interhabitat comparisons in tidal freshwater environments are limited to studies comparing nekton use between SAV and unvegetated bottom (Rozas and Odum 1987a) or between tidal creeks and the marsh surface (Rozas et al. 1988).

The objective of my study was to directly compare fish and decapod crustacean densities in shallow subtidal and low intertidal habitats of a tidal freshwater system. In this chapter, I document the relative value of major tidal freshwater habitats for nekton in the Atchafalaya River Delta by comparing nekton densities among SAV, marsh edge, and unvegetated bottom. In addition, I describe the composition, relative abundance, and seasonal abundance of nekton associated with these habitats.

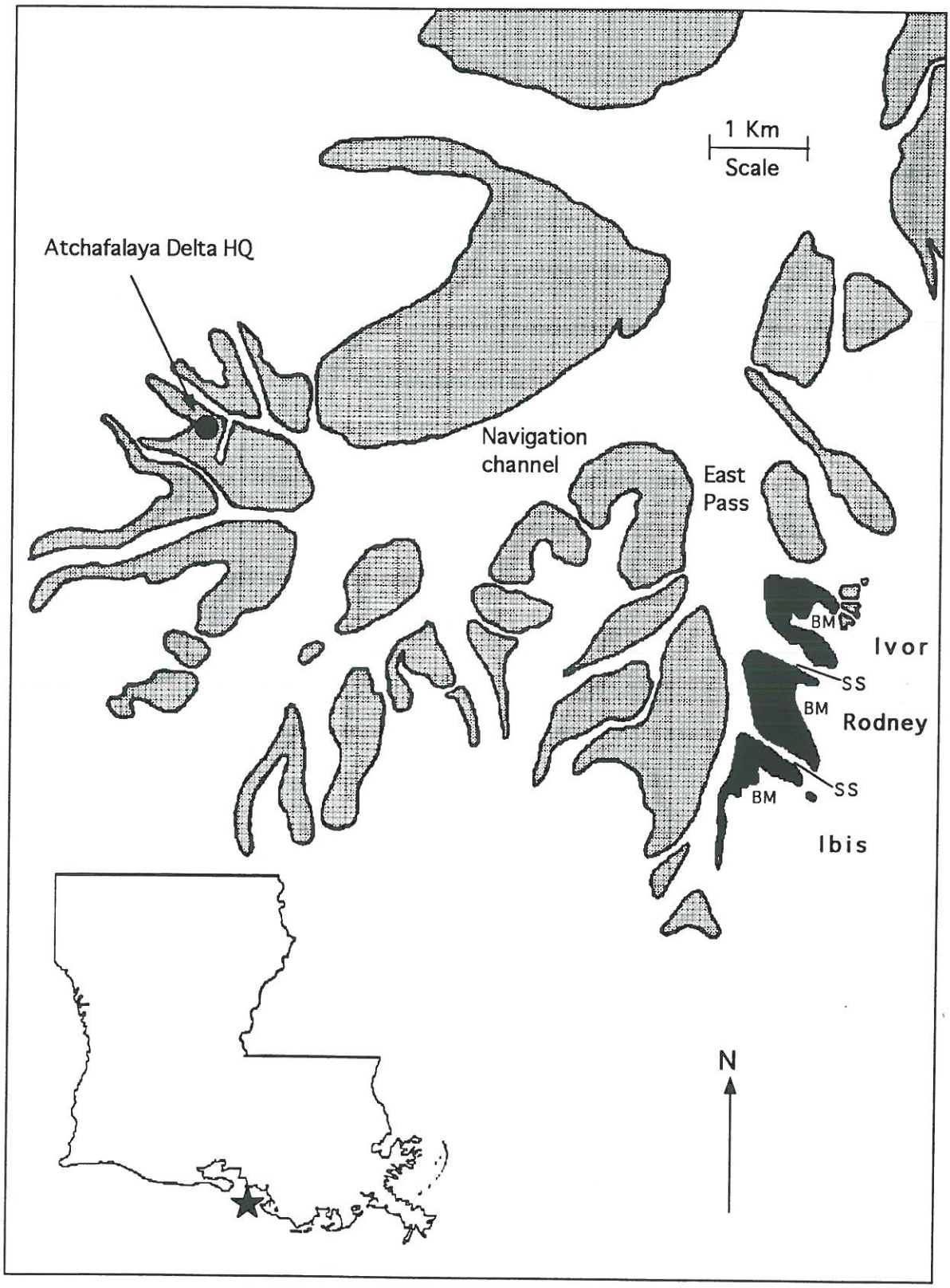
MATERIALS AND METHODS

Study area

The study area is within the Atchafalaya River Delta located approximately 32 km south of Morgan City, Louisiana near latitude 29^0 N and longitude 91^0 W (Fig. 1.1). Atchafalaya River flow controls salinities in the delta; during most of the year, salinities in Atchafalaya Bay are below 0.5 ppt (Orlando et al. 1993). Tides are predominantly diurnal and have a mean range of 0.2 m (U. S. Department of Commerce 1993); however, tidal effects may be overridden by meteorological factors or when river outflow is high. Typically, water temperatures in Atchafalaya Bay are below 15^0C from December through early March and above 25^0C from May through September. Bay water is cooler than waters of surrounding bays during normal Atchafalaya River flows and up to 10^0C cooler during high river discharge (Hoese 1976).

I selected sample sites on three natural islands (Ivor, Rodney, Ibis) located on the east side of East Pass (Fig. 1.1). The diverse vegetation on and around these islands consisted of at least 10 species of SAV and at least seven species of emergent macrophytes (pers. obs.). Submerged aquatic vegetation occurred both in the subtidal and lowest intertidal areas and was dominated by Potamogeton nodosus and Najas guadalupensis. Other species of SAV (e.g. Vallisneria americana and Heteranthera dubia) were much less abundant and occurred only in widely scattered patches. Emergent vegetation was dominated by Scirpus americanus, and additionally in the fall by Sagittaria platyphylla and Sagittaria latifolia. Sparse stands of S. platyphylla occurred in the low intertidal; this species was replaced by S. latifolia at slightly higher elevations. Dense, monospecific stands of Scirpus occupied the highest intertidal areas. All habitats occurred in the "backmarsh" of each island, the side of the island opposite East pass and therefore protected from direct river flow (Fig. 1.1). Scirpus also occurred on island streamsides along secondary river channels. Marsh and SAV habitats were present from May through October. However, the areal coverage of habitats varied seasonally from spring

Figure 1.1 Map of the study area showing its location along the Louisiana coast. I sampled six habitats among the three islands shown in black. Backmarsh (BM) habitats occur behind the islands, whereas streamside (SS) habitat is present along the south side of channels between Ivor Island and Rodney Island and between Rodney Island and Ibis Island. The Amerada Hess tide gauge is located at the LA Department of Wildlife and Fisheries Atchafalaya Delta headquarters (HQ).


1 Km
Scale
Atchafalaya Delta HQ
Navigation
channel
East
Pass
BM
Ivor
SS
BM
Rodney
BM
SS
Ibis
N

through fall. During winter months, the vegetation disappears because of either natural senescence or consumption by waterfowl.

Methods

I randomly sampled six major shallow-water habitats including two dominated by SAV (Potamogeton and Najas), three dominated by emergent vegetation (Sagittaria spp., backmarsh Scirpus, and streamside Scirpus), and unvegetated bottom. Sagittaria marsh consisted of mixed stands of S. platyphylla and S. latifolia; these species were treated as one habitat because herbivory by nutria Myocastor coypus made distinguishing between the species difficult. The two species, when grazed by nutria, become morphologically similar. Each month, I selected the most abundant habitats in the study area to sample (Table 1).

I sampled nekton (fishes and decapod crustaceans) at high tide when all habitats were flooded, and therefore available to aquatic organisms, using a 1 m^2 aluminum throw trap (Kushlan 1981, Rozas and Odum 1987a). The throw trap provides a standard quantitative sample in shallow water, performs similarly in vegetated and unvegetated habitats, and does not have the bias of permanent samplers caused by added structure in unvegetated habitats (Rozas and Minello 1997; Jordan et al. in review).

Sample sites were slowly approached in a small, unpowered, aluminum boat. When approximately 3 m from the sample site, I threw the trap from the bow of the boat. The trap was pushed into the sediment and checked for complete contact with the substrate. Prior to removal of animals trapped inside the sampler, I measured salinity and water temperature inside the trap with a Rosemount ® RS5-3 portable salinometer. I measured water depth inside the sampler with a meter stick. Vegetation inside the enclosure was clipped at the sediment surface and removed. I collected animals by sweeping the inside of the trap ten times with a bar seine that fit exactly inside the enclosure walls.

Nekton samples were preserved in 10% formalin. In the laboratory, samples were rinsed for at least 24 h before separating animals from plant parts. Animals were identified,

Table 1.1 Months in which habitats occupied a substantial portion of the study area and therefore were sampled. Islands where habitats were sampled are indicated as follows: I = Ivor, R = Rodney, and B = Ibis.

		Habitat					
Month	Season	*Potamogeton nodosus*	*Najas guadalupensis*	backmarsh *Scirpus americanus*	streamside *Scirpus americanus*	*Sagittaria*	Unvegetated
July(1994)	Summer	I,R,B	I,R,B	R,B	R,B		
August		I,R,B	I,R,B	R,B	R,B		
September	Fall	I,R,B		R,B		I,R,B	I,R,B
October		I,R,B		R,B		I,R,B	I,R,B
May (1995)	Spring	I,R,B		R,B	R,B		I,R,B
June		I,R,B	I,R,B	R,B	R,B		I,R,B

counted, and weighed by species (nearest 0.1g wet weight). The standard length of fishes and total length of crustaceans (rostrum to telson for shrimp, carapace width for crabs) were measured to the nearest millimeter.

Vegetation biomass and stem density (for emergents only) was determined from the vegetation removed from the trap at marsh and SAV sites. In the laboratory, I sorted vegetation by species, recorded a wet weight, and dried samples at 60 ^{0}C for two weeks to a constant weight. For large samples, only a subsample (25% of wet weight) was dried, weighed, and used to estimate the dry weight of the entire sample.

On the basis of a preliminary study for estimating sample size (described below), each month (July-October 1994 and May-June 1995) I sampled each habitat dominant in the study area 12 times (Table 1.1). I sampled Potamogeton and backmarsh Scirpus every month during the sampling period (total = six months), streamside Scirpus and unvegetated bottom four months, Najas three months, and Sagittaria two months. Most habitats occurred at all three islands in the study area, and therefore, each month, I took samples of these habitats at all three islands. However, I sampled backmarsh and streamside Scirpus only at Rodney Island and Ibis Island as Scirpus marsh was confined to these two islands.

I estimated sample size (number of samples) necessary to detect differences in nekton density among habitats using data from a pilot study conducted in June 1994. At least 16 samples were taken in each of three habitats (Potamogeton, Najas, and backmarsh Scirpus). I calculated sample variance using data for fish and decapod crustaceans taken in the pilot study. Sample size was estimated using an iterative process outlined in Sokal and Rohlf (1995).

I conducted an experiment to estimate the efficiency of removing animals from the throw trap using individuals of two species (sheepshead minnow Cyprinodon variegatus and Ohio shrimp Macrobrachium ohione). I marked fish by clipping their anal fin and shrimp by removing the tip of their telson. Animals were released into the trap after it was deployed in either SAV (Potamogeton) or marsh (Scirpus) and allowed to acclimate for approximately two minutes before the vegetation was removed. I removed animals from the trap using the

procedure described above; however, samples from each sweep of the net were collected and analyzed separately.

I obtained hourly water level readings for the Atchafalaya Bay near Eugene Island (LA) tide gauge # 88550 (Amerada Hess production platform) for January 1994 - December 1995 from the U.S. Army Corps of Engineers, New Orleans District. The gauge is located approximately 5.8 km west of the study area near the Atchafalaya Delta Wildlife Management Area headquarters (Fig. 1.1). I estimated the elevation of each sample site relative to the tide gauge by calculating the difference between water depth measurements at each site and concurrent tide gauge readings from the Amerada Hess gauge. I then used site elevations (relative to the gauge) and tide gauge data to calculate monthly mean flooding durations (percentage of time the habitat was submerged) for each habitat.

Statistical analyses

I considered consecutive months in which I sampled the same habitats as a single sampling period or season. Therefore, I considered July and August as summer, September and October as fall, and May and June as the spring. Data for each season were analyzed separately because the habitats I sampled were only consistent within a season, and because some important nekton species were only abundant enough for statistical analysis in one season. I used a multivariate analysis of variance (MANOVA) to test the null hypothesis that mean densities of numerically dominant species examined simultaneously are equal among habitats, and separate, univariate analysis of variance (3-way ANOVA; GLM procedure) tests following significant MANOVA results (protected ANOVA) to test the null hypothesis for individual species. I used the same statistical tests (MANOVA followed by separate ANOVA) to test the null hypothesis that mean environmental parameter values (salinity, water temperature, water depth, elevation) and mean vegetation biomasses are equal among all habitats. I also used an ANOVA to test the null hypothesis that mean densities of total fishes and total crustaceans are equal among habitats. Habitat was the main effect (with 4 levels); the

blocking factors, month and island, had two and three levels, respectively. Following a significant ANOVA analysis, means of specific habitats were compared with the Least Square Means Test because the data were not completely balanced. All data were transformed using the Box-Cox procedure to improve normality and make the variances homogeneous prior to analysis. I used Pearson correlations to examine the relationships between animal densities and physical parameters and between animal densities and vegetation biomass. An alpha level of 0.05 was used for the MANOVA and ANOVA, but alpha was adjusted by the Bonferroni method (0.05 divided by the number of comparisons) for Least Square Means Tests and Pearson correlations to reduce the error introduced by making multiple comparisons. All statistical analyses were performed using SAS (SAS Institute, 1989).

RESULTS

In 298 samples, I collected a total of 26 fish species and 5 crustacean species in summer, 17 species of fishes and 7 species of crustaceans in fall, and 18 species of fishes and 4 species of crustaceans in spring (Table 1.2). Fishes represented >65% of the total nekton collected, and most were taken in summer (2121) and fall (2008). Many fewer fishes were collected in the spring (218). The total catch of crustaceans was highest in the fall (1491), largely due to an influx of juvenile blue crabs into the study area; crustaceans were less than half as numerous in either summer (539) or spring (249) than fall (Table 1.2).

Mean densities of numerically dominant species (tested simultaneously) were significantly different among habitats in summer (Wilks' Lambda = 0.26, $F_{21,233} = 6.74$; $p < 0.0001$), fall (Wilks' Lambda = 0.25, $F_{21,239} = 6.99$; $p < 0.0001$), and spring (Wilks' Lambda = 0.34, $F_{28,340} = 4.22$; $p<0.0001$).

Table 1.2 Mean density (number per m^2) and S.E. (one standard error), untransformed data, of fishes and crustaceans taken in each habitat sampled during each season. The total catch (total number of animals collected in all habitats combined) and number of fish and crustacean species collected are also listed. Each mean was calculated from 24 samples except 22 samples for streamside Scirpus in Summer 1994 and 12 for Najas in Spring 1995. Relative abundance (RA) is given for those species with at least 1% relative abundance. Results (P values) of MANOVA and ANOVA tests (considered significant at $p<0.05$) comparing mean densities among habitats within a season are given for each taxa included in the analyses. Blank spaces represent seasons in which habitats were not dominant and therefore not sampled.

	Potamogeton nodosus		Najas guadalupensis		backmarsh Scirpus americanus		streamside Scirpus americanus		Sagittaria		Unvegetated		Total		MANOVA Wilks' Lambda	ANOVA
Species	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Catch	RA (%)	P value	P value
Summer 1994																
Fishes (Total spp.=26)															0.0001	
Number of species	3.1	(0.24)	2.9	(0.16)	3.4	(0.31)	2.3	(0.33)								
Sheepshead minnow Cyprinodon variegatus	11.5	(2.98)	17.6	(6.77)	15.0	(3.75)	0.5	(0.31)								
Rainwater killifish Lucania parva	10.0	(1.72)	10.8	(2.42)	7.8	(2.47)	1.3	(0.49)					1070	50.4		0.0001
Inland silverside Menidia beryllina	0.4	(0.20)	0.0	(0.04)	2.2	(0.77)	0.1	(0.09)					716	33.8		0.0001
Freshwater goby Gobionellus shufeldti	0.4	(0.21)	0.2	(0.10)	0.7	(0.51)	1.5	(0.72)					65	3.1		0.0001
Gulf killifish Fundulus grandis	0.5	(0.21)	0.0	(0.04)	1.2	(0.31)	0.8	(0.35)					64	3.0		0.0015
Western mosquitofish Gambusia affinis	0.2	(0.43)	0.6	(0.42)	0.3	(0.17)	0.7	(0.46)					61	2.9		
Speckled worm eel Myrophis punctatus	0.5	(0.16)	0.4	(0.12)	0.1	(0.07)	0.2	(0.13)					41	1.9		
Least killifish Heterandria formosa	0.1	(0.06)	0.0	(0.04)	0.3	(0.21)	0.6	(0.35)					29	1.4		
Bay anchovy Anchoa mitchilli	0.0	(0.00)	0.2	(0.13)	0.2	(0.17)	0.1	(0.05)					23	1.1		
Striped mullet Mugil cephalus	0.0	(0.00)	0.3	(0.33)	0.0	(0.00)	0.0	(0.00)					9			
Fat sleeper Dormitator maculatus	0.0	(0.00)	0.1	(0.08)	0.0	(0.04)	0.1	(0.08)					8			
Gizzard shad Dorosoma cepedianum	0.0	(0.00)	0.1	(0.07)	0.1	(0.08)	0.0	(0.00)					6			
Fundulus sp.	0.0	(0.04)	0.1	(0.08)	0.1	(0.08)	0.0	(0.00)					5			
Bluegill Lepomis macrochirus	0.1	(0.13)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					5			
Spotted bass Micropterus punctulatus	0.1	(0.08)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					3			
Spotted gar Lepisosteus oculatus	0.1	(0.06)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					2			
Gobiidae sp.	0.0	(0.00)	0.0	(0.00)	0.0	(0.04)	0.0	(0.05)					2			
Darter goby Gobionellus boleosoma	0.1	(0.06)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					2			
Highfin goby Gobionellus oceanicus	0.0	(0.00)	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)					2			
Lyre goby Evorthodus lyricus	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.05)					1			
Rough silverside Membras martinica	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)					1			
Ladyfish Elops saurus	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)					1			
Banded pygmy sunfish Elassoma zonatum	0.0	(0.00)	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)					1			
Hogchoker Trinectes maculatus	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.05)					1			
Golden topminnow Fundulus chrysotus	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.05)					1			
Sciaenidae sp.	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.05)					1			
TOTAL FISHES	24.0	(3.40)	30.5	(7.49)	28.2	(4.94)	6.2	(0.98)					2121			0.0001
Crustaceans (Total spp.=5)																
Number of species	1.6	(0.17)	0.6	(0.12)	1.0	(0.17)	1.0	(0.23)								
Riverine grass shrimp Palaemonetes paludosus	7.6	(3.44)	0.8	(0.49)	0.3	(0.15)	1.2	(0.70)					233	43.2		0.0081
Blue crab Callinectes sapidus	4.9	(1.23)	1.0	(0.37)	3.3	(0.96)	0.4	(0.16)					228	42.3		0.0001
Ohio shrimp Macrobrachium ohione	0.5	(0.27)	0.0	(0.00)	1.8	(1.75)	0.2	(0.11)					61	11.3		0.1307
Crayfish spp.	0.2	(0.13)	0.2	(0.17)	0.0	(0.04)	0.0	(0.05)					11	2.0		
Uca spp.	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.3	(0.15)					6	1.1		
TOTAL CRUSTACEANS	13.2	(3.62)	2.0	(0.57)	5.4	(1.96)	2.1	(0.78)					539			0.0002

Table 1.2 (Continued)

Species	Potamogeton nodosus Mean	Potamogeton nodosus S.E.	Najas guadalupensis Mean	Najas guadalupensis S.E.	backmarsh Scirpus americanus Mean	backmarsh Scirpus americanus S.E.	streamside Scirpus americanus Mean	streamside Scirpus americanus S.E.	Sagittaria Mean	Sagittaria S.E.	Unvegetated Mean	Unvegetated S.E.	Total Catch	RA (%)	MANOVA Wilks' Lambda P value	ANOVA P value
Fall 1994															0.0001	
Fishes (Total spp.=17)																
Number of species	3.3	(0.21)			3.1	(0.28)			3.3	(0.22)	1.5	(0.22)				
Sheepshead minnow Cyprinodon variegatus	10.0	(2.43)			22.7	(4.87)			15.5	(5.72)	0.3	(0.16)	1164	58.0		0.0001
Rainwater killifish Lucania parva	6.7	(1.49)			3.6	(1.30)			8.1	(2.69)	0.1	(0.09)	445	22.2		0.0001
Bay anchovy Anchoa mitchilli	1.8	(1.06)			0.7	(0.33)			0.7	(0.44)	1.8	(0.70)	120	6.0		0.0096
Inland silverside Menidia beryllina	0.6	(0.27)			1.8	(0.61)			2.0	(0.75)	0.5	(0.26)	116	5.8		0.0277
Darter goby Gobionellus boleosoma	1.0	(0.29)			0.1	(0.09)			0.7	(0.29)	0.2	(0.10)	49	2.4		
Western mosquito fish Gambusia affinis	0.1	(0.07)			0.8	(0.75)			0.1	(0.07)	0.0	(0.00)	26	1.3		
Gobionellus sp.	0.8	(0.83)			0.0	(0.00)			0.0	(0.00)	0.0	(0.00)	20	1.0		
Highfin goby Gobionellus oceanicus	0.1	(0.07)			0.0	(0.00)			0.2	(0.10)	0.3	(0.14)	13			
Gulf killifish Fundulus grandis	0.1	(0.08)			0.2	(0.10)			0.2	(0.17)	0.0	(0.00)	11			
Speckled worm eel Myrophis punctatus	0.2	(0.10)			0.1	(0.06)			0.1	(0.06)	0.0	(0.04)	10			
Freshwater goby Gobionellus shufeldti	0.1	(0.06)			0.2	(0.13)			0.1	(0.06)	0.0	(0.00)	9			
Least killifish Heterandria formosa	0.0	(0.00)			0.1	(0.08)			0.2	(0.15)	0.0	(0.00)	7			
Striped mullet Mugil cephalus	0.0	(0.00)			0.1	(0.09)			0.0	(0.04)	0.1	(0.09)	7			
Fundulus sp.	0.0	(0.00)			0.0	(0.04)			0.3	(0.14)	0.0	(0.00)	7			
Gerridae sp.	0.0	(0.00)			0.0	(0.00)			0.0	(0.04)	0.0	(0.04)	2			
Atlantic needlefish Strongylura marina	0.0	(0.00)			0.0	(0.04)			0.0	(0.00)	0.0	(0.00)	1			
Fat sleeper Dormitator maculatus	0.0	(0.00)			0.0	(0.04)			0.0	(0.00)	0.0	(0.00)	1			
TOTAL FISHES	21.5	(3.18)			30.5	(5.56)			28.3	(6.04)	3.4	(0.81)	2008			0.0001
Crustaceans (Total spp.=7)																
Number of species	2.0	(0.17)			2.0	(0.26)			2.0	(0.22)	1.7	(0.12)				
Blue crab Callinectes sapidus	16.9	(3.19)			11.5	(3.20)			13.5	(1.89)	1.4	(0.40)	1039	69.7		0.0001
Riverine grass shrimp Palaemonetes paludosus	4.2	(1.81)			0.9	(0.39)			3.5	(1.64)	0.1	(0.13)	210	14.1		0.0016
Ohio shrimp Macrobrachium ohione	2.1	(0.66)			1.7	(1.07)			4.8	(2.68)	0.1	(0.08)	209	14.0		0.0044
Crayfish spp.	0.0	(0.00)			0.3	(0.19)			0.7	(0.33)	0.0	(0.00)	24	1.6		
Uca sp.	0.0	(0.00)			0.2	(0.17)			0.0	(0.00)	0.0	(0.00)	5			
Crab sp.	0.0	(0.00)			0.1	(0.07)			0.0	(0.00)	0.0	(0.00)	3			
Shrimp sp.	0.0	(0.00)			0.0	(0.04)			0.0	(0.00)	0.0	(0.00)	1			
TOTAL CRUSTACEANS	23.2	(3.88)			14.9	(3.83)			22.5	(4.70)	1.6	(0.44)	1491			0.0001

Table 1.2 (Continued).

Species	Potamogeton nodosus Mean	S.E.	Najas guadalupensis Mean	S.E.	backmarsh Scirpus americanus Mean	S.E.	streamside Scirpus americanus Mean	S.E.	Sagittaria Mean	S.E.	Unvegetated Mean	S.E.	Total Catch	RA (%)	MANOVA Wilks' Lambda P value	ANOVA P value
Spring 1995																
Fishes (Total spp.=18)															0.0001	
Number of species	1.8	(0.21)	1.7	(0.38)	1.0	(0.17)	1.2	(0.23)			0.8	(0.17)				
Bay Anchovy Anchoa mitchilli	0.7	(0.44)	1.2	(0.58)	0.5	(0.23)	0.8	(0.53)			0.6	(0.25)	75	34.4		0.8244
Freshwater goby Gobionellus shufeldti	0.3	(0.13)	0.3	(0.13)	0.3	(0.13)	0.8	(0.20)			0.1	(0.07)	38	17.4		0.0758
Speckled worm eel Myrophis punctatus	0.7	(0.17)	0.4	(0.15)	0.1	(0.09)	0.2	(0.08)			0.1	(0.07)	31	14.2		0.0065
Darter goby Gobionellus boleosoma	0.2	(0.10)	0.7	(0.26)	0.2	(0.10)	0.1	(0.09)			0.1	(0.06)	21	9.6		0.0302
Striped mullet Mugil cephalus	0.2	(0.08)	0.1	(0.08)	0.0	(0.00)	0.3	(0.22)			0.0	(0.04)	13	6.0		
Inland silverside Menidia beryllina	0.2	(0.10)	0.0	(0.00)	0.2	(0.10)	0.0	(0.04)			0.0	(0.04)	11	5.0		
Bay whiff Citharichthys spilopterus	0.0	(0.04)	0.0	(0.00)	0.1	(0.06)	0.2	(0.08)			0.1	(0.06)	9	4.1		
Sheepshead minnow Cyprinodon variegatus	0.1	(0.06)	0.0	(0.00)	0.1	(0.08)	0.0	(0.04)			0.0	(0.00)	5	2.3		
Rainwater killifish Lucania parva	0.0	(0.00)	0.2	(0.11)	0.0	(0.04)	0.0	(0.00)			0.0	(0.00)	3	1.4		
Gobionellus sp.	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)	0.0	(0.04)			0.0	(0.00)	2			
Lyre goby Evorthodus lyricus	0.1	(0.06)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)			0.0	(0.00)	2			
Southern flounder Paralichthys lethostigma	0.1	(0.06)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)			0.0	(0.00)	2			
Spot Leiostomus xanthurus	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)			0.0	(0.00)	1			
Atlantic croaker Micropogonias undulatus	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)			0.0	(0.04)	1			
Syngnathus sp.	0.0	(0.04)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)			0.0	(0.00)	1			
Banded pygmy sunfish Elassoma zonatum	0.0	(0.00)	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)			0.0	(0.00)	1			
Gizzard shad Dorosoma cepedianum	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)			0.0	(0.04)	1			
Least killifish Heterandria formosa	0.0	(0.00)	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)			0.0	(0.00)	1			
TOTAL FISHES	2.6	(0.44)	2.8	(0.73)	1.5	(0.30)	2.4	(0.68)			1.2	(0.31)	218			0.0163
Crustaceans (Total spp.=4)																
Number of species	1.8	(0.18)	0.9	(0.23)	0.5	(0.13)	0.6	(0.17)			0.2	(0.09)				
Ohio shrimp Macrobrachium ohione	3.2	(2.14)	1.0	(0.52)	0.1	(0.06)	1.7	(1.11)			0.0	(0.00)	130	52.2		0.0001
Blue crab Callinectes sapidus	2.4	(0.34)	0.6	(0.26)	0.5	(0.18)	0.4	(0.16)			0.2	(0.09)	92	36.9		0.0001
Riverine grass shrimp Palaemonetes paludosus	0.6	(0.19)	0.1	(0.08)	0.0	(0.04)	0.4	(0.22)			0.0	(0.00)	26	10.4		0.0009
Crawfish sp.	0.0	(0.00)	0.0	(0.00)	0.0	(0.04)	0.0	(0.00)			0.0	(0.00)	1			
TOTAL CRUSTACEANS	6.2	(2.26)	1.7	(0.63)	0.7	(0.21)	2.5	(1.36)			0.2	(0.09)	249			0.0001

Habitat use: summer

In summer 1994, Najas reached a peak in areal coverage, and formed extensive beds over much of the intertidal and shallow subtidal areas of the study area. Potamogeton habitat also was prevalent at this time, but occurred as numerous isolated beds scattered throughout the study area. Scirpus was well established in both backmarsh and streamside areas.

Sheepshead minnows, rainwater killifish Lucania parva, inland silversides Menidia beryllina, and freshwater gobies Gobionellus shufeldti were numerically dominant in summer and accounted for 90% of the fishes collected at this time (Table 1.2). Mean densities of total fishes were nearly evenly distributed among backmarsh habitats and significantly greater in these habitats than in streamside Scirpus (Fig. 1.2a, Table 1.3). This overall pattern for fishes was largely due to the distribution of sheepshead minnows and rainwater killifish, which represented >84% of the fishes collected in summer (Fig. 1.2b, Table 1.2). Inland silversides and freshwater gobies were much less abundant overall (6% of total) and exhibited a different distributional pattern than sheepshead minnows and rainwater killifish. Inland silversides and freshwater gobies were most abundant in Scirpus marsh (Fig. 1.2b, Tables 2 and 3); inland silversides were significantly more abundant in backmarsh Scirpus than all other habitats, whereas freshwater gobies were significantly more abundant in streamside Scirpus than other habitats (Fig. 1.2b, Table 1.3).

Numerically dominant crustaceans in summer were riverine grass shrimp Palaemonetes paludosus, blue crabs Callinectes sapidus, and Ohio shrimp, accounting for >96% of the summer catch (Table 1.2). Total crustacean mean densities were significantly higher in Potamogeton than in streamside Scirpus or Najas but densities in Potamogeton and backmarsh Scirpus were not significantly different (Fig. 1.2a, Table 1.3). Blue crab mean densities were not different between Potamogeton and backmarsh Scirpus, and densities were significantly greater in these habitats than in Najas or streamside Scirpus (Fig. 1.2c, Table 1.3). Riverine grass shrimp were significantly more abundant in Potamogeton than Najas, but densities in Potamogeton, streamside Scirpus, and backmarsh Scirpus were not significantly different.

Figure 1.2a Mean density (individuals/m^2) of total fishes and total crustaceans, collected in summer 1994 from Potamogeton, Najas, backmarsh Scirpus, and streamside Scirpus habitats. Least Square Means and confidence limits of transformed data were calculated from 22 samples for streamside Scirpus and 24 samples for all other habitats. Back-transformed means and confidence limits are presented. Error bars = 95% confidence interval.

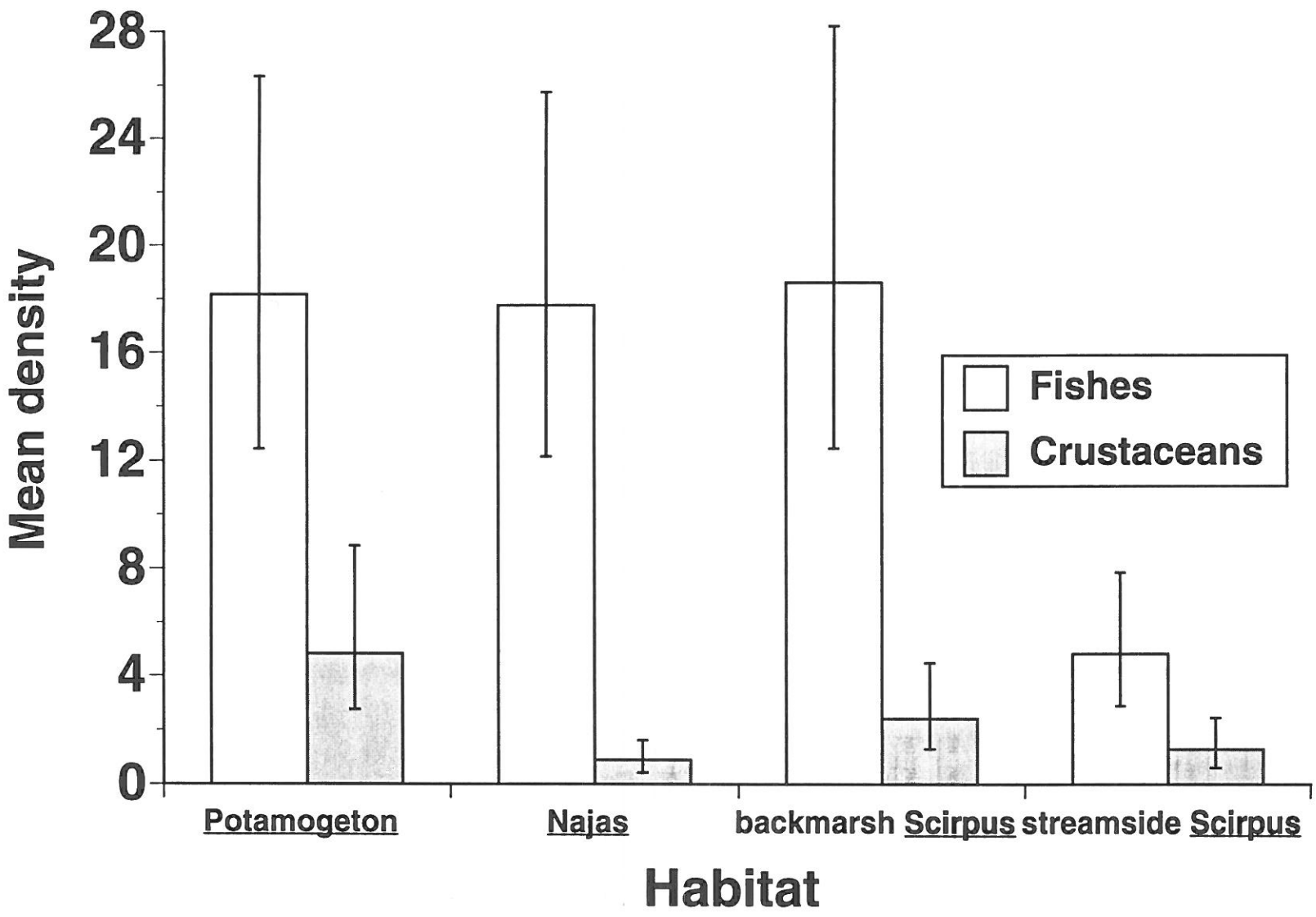

Mean density
28
24
20
16
12
8
4
0
Fishes
Crustaceans
Potamogeton
Najas
backmarsh Scirpus
streamside Scirpus
Habitat

Table 1.3 Results of Least Square Means comparison tests following significant ($p < 0.05$) ANOVA test results. Nonsignificant ANOVA tests are indicated by "NS". Habitats are listed in descending order of mean animal density. Means that did not differ significantly at $p < 0.0083$ ($p < 0.005$ for spring) are joined by a line (—). Habitats are represented as follows: PN=Potamogeton nodosus, NG=Najas guadalupensis, BSA=backmarsh Scirpus americanus, SSA=streamside Scirpus americanus, SG=Sagittaria, and UN=unvegetated. Blank spaces represent seasons in which species were not dominant and therefore not included in the analysis.

Taxa	Habitat Summer 1994	Fall 1994	Spring 1995
Total Fishes	BSA PN NG SSA	BSA SG PN UN	PN NG SSA BSA UN
Sheepshead minnow Cyprinodon variegatus	PN NG BSA SSA	BSA PN SG UN	
Rainwater killifish Lucania parva	PN NG BSA SSA	PN SG BSA UN	
Inland silverside Menidia beryllina	BSA PN SSA NG	BSA SG PN UN	
Freshwater goby Gobionellus shufeldti	SSA BSA PN NG		NS
Bay anchovy Anchoa mitchilli		UN PN BSA SG	NS
Speckled worm eel Myrophis punctatus			PN NG SSA BSA UN
Darter goby Gobionellus boleosoma			NG PN BSA UN SSA
Total crustaceans	PN BSA SSA NG	PN SG BSA UN	PN NG SSA BSA UN *
Blue crab Callinectes sapidus	PN BSA NG SSA	PN SG BSA UN	PN NG BSA SSA UN
Riverine grass shrimp Palaemonetes paludosus	PN SSA BSA NG	PN SG BSA UN	PN SSA BSA UN NG
Ohio shrimp Macrobrachium ohione	NS	PN BSA SG UN	PN NG SSA BSA UN

* According to the Least Square Means test, UN is actually significantly different from PN and SSA, but not different from NG or BSA.

Figure 1.2b Mean density (individuals/m^2) of sheepshead minnow Cyprinodon variegatus, rainwater killifish Lucania parva, inland silverside Menidia beryllina, and freshwater goby Gobionellus shufeldti collected in summer 1994 from Potamogeton, Najas, backmarsh Scirpus, and streamside Scirpus habitats. Least Square Means and confidence limits of transformed data were calculated from 22 samples for streamside Scirpus and 24 samples for all other habitats. Back-transformed means and confidence limits are presented. Error bars = 95% confidence interval.

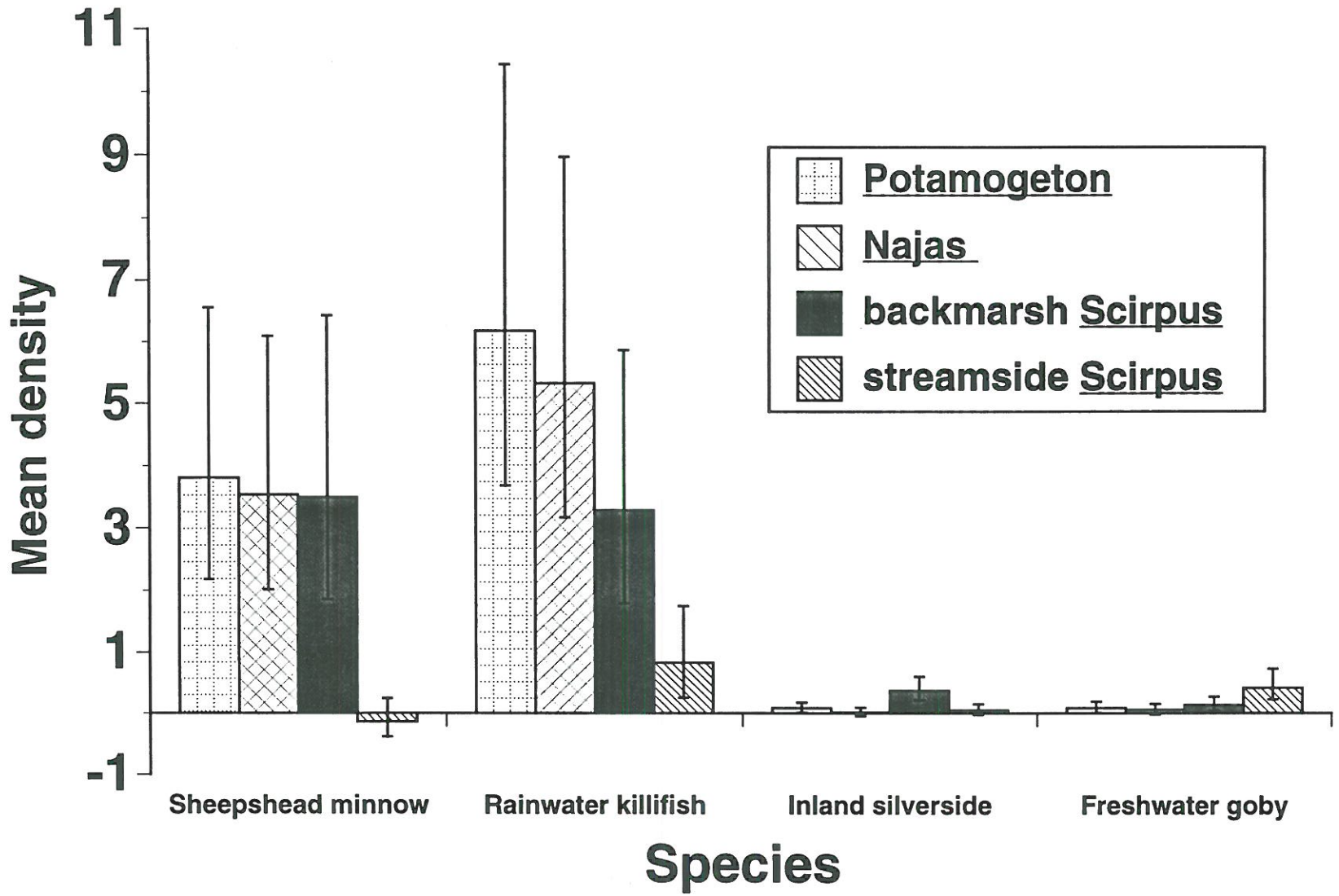
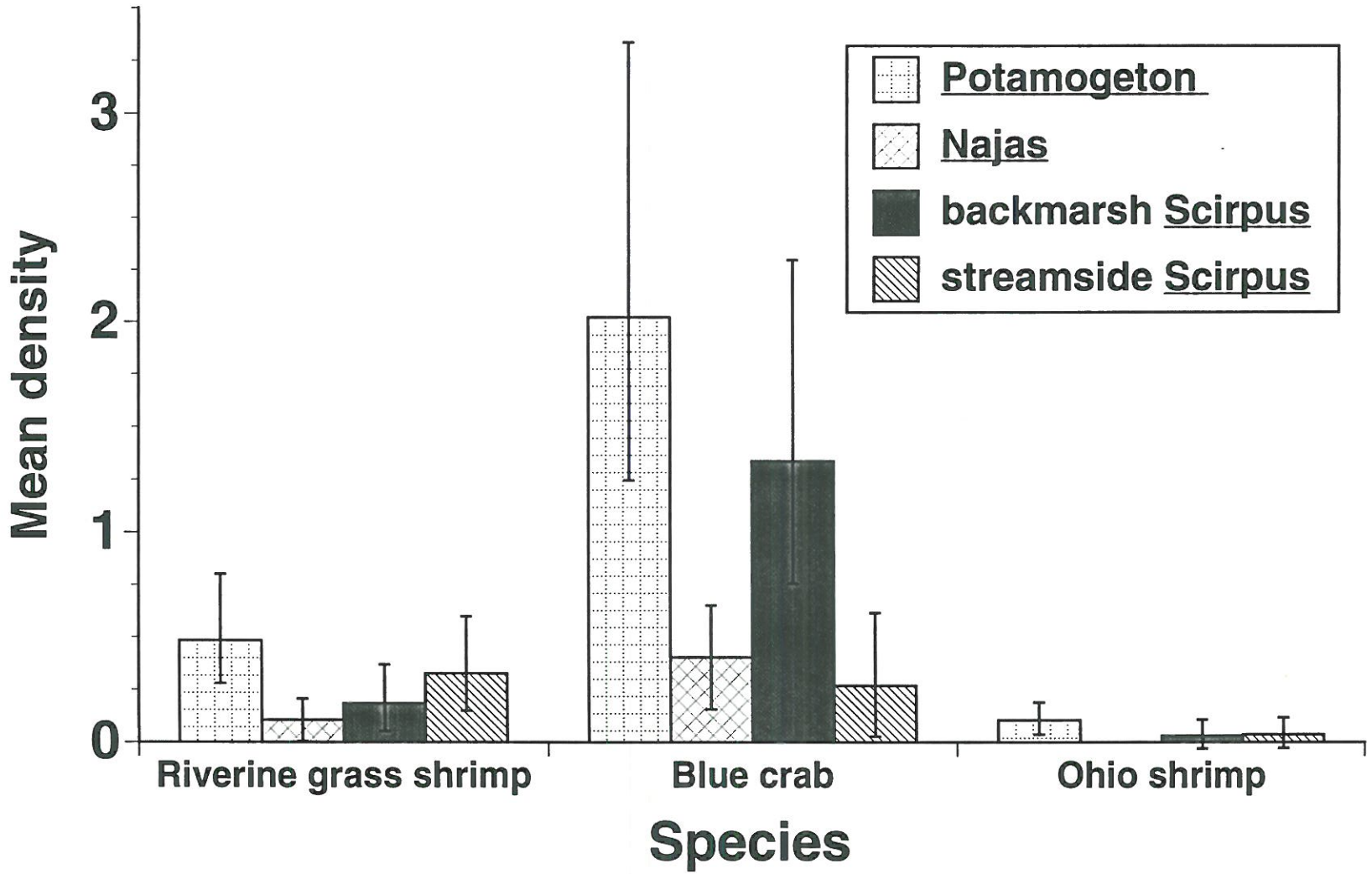

11
9
7
5
3
1
-1
Mean density
Potamogeton
Najas
backmarsh Scirpus
streamside Scirpus
Sheepshead minnow
Rainwater killifish
Inland silverside
Freshwater goby
Species

Figure 1.2c Mean density (individuals/m^2) of riverine grass shrimp Palaemonetes paludosus, blue crab Callinectes sapidus, and Ohio shrimp Macrobrachium ohione collected in summer 1994 from Potamogeton, Najas, backmarsh Scirpus, and streamside Scirpus habitats. Least Square Means and confidence limits of transformed data were calculated from 22 samples for streamside Scirpus and 24 samples for all other habitats. Back-transformed means and confidence limits are presented. Error bars = 95% confidence interval.


Potamogeton
Najas
backmarsh Scirpus
streamside Scirpus
Mean density
0
1
2
3
Riverine grass shrimp
Blue crab
Ohio shrimp
Species

Ohio shrimp were not collected at all from Najas; however, densities did not differ statistically among habitats.

Habitat use: fall

In fall 1994, Najas began to die off, leaving large areas of unvegetated mud bottom. Potamogeton was still present but in slightly smaller patches than in summer. Sagittaria habitat occurred in backmarsh areas as dense, isolated patches (Ivor Island) or sparsely scattered over large areas (Rodney and Ibis Islands). Streamside Scirpus was still present, but inaccessible for sampling because wide, dense bands of water hyacinth Eichhornia crassipes had stranded at the edge of the marsh.

Sheepshead minnows, rainwater killifish, bay anchovies Anchoa mitchilli, and inland silversides were numerically dominant in fall and accounted for 92% of the fishes collected (Table 1.2). During fall, densities of total fish, sheepshead minnows, and rainwater killifish were significantly greater in vegetated than unvegetated habitat, but densities among the vegetated habitats were not significantly different (Fig. 1.3a, Table 1.3). In contrast, bay anchovies were significantly more abundant in unvegetated habitat than backmarsh Scirpus or Sagittaria habitats, but densities in unvegetated habitat and Potamogeton were not significantly different (Fig. 1.3b, Table 1.3). Although the ANOVA was significant, densities of inland silversides were not significantly different among habitats according to Least Square Means comparisons (Table 1.3).

Blue crabs, riverine grass shrimp, and Ohio shrimp were the numerically dominant species in fall as in summer, accounting for >97% of total crustaceans collected (Table 1.2). Mean densities of total crustaceans, as well as blue crabs and riverine grass shrimp, were significantly greater in all vegetated habitats than on unvegetated bottom; however, densities of these taxa were not significantly different among vegetated habitats (Figs. 3a and 3c, Table 1.3). Ohio shrimp were significantly more abundant in Potamogeton than unvegetated habitat,

Figure 1.3a Mean density (individuals/m^2) of total fishes and total crustaceans collected in fall 1994 from Potamogeton, backmarsh Scirpus, Sagittaria, and unvegetated habitats. Least Square Means and confidence limits of transformed data were calculated from 24 samples. Back-transformed means and confidence limits are presented. Error bars = 95% confidence interval.

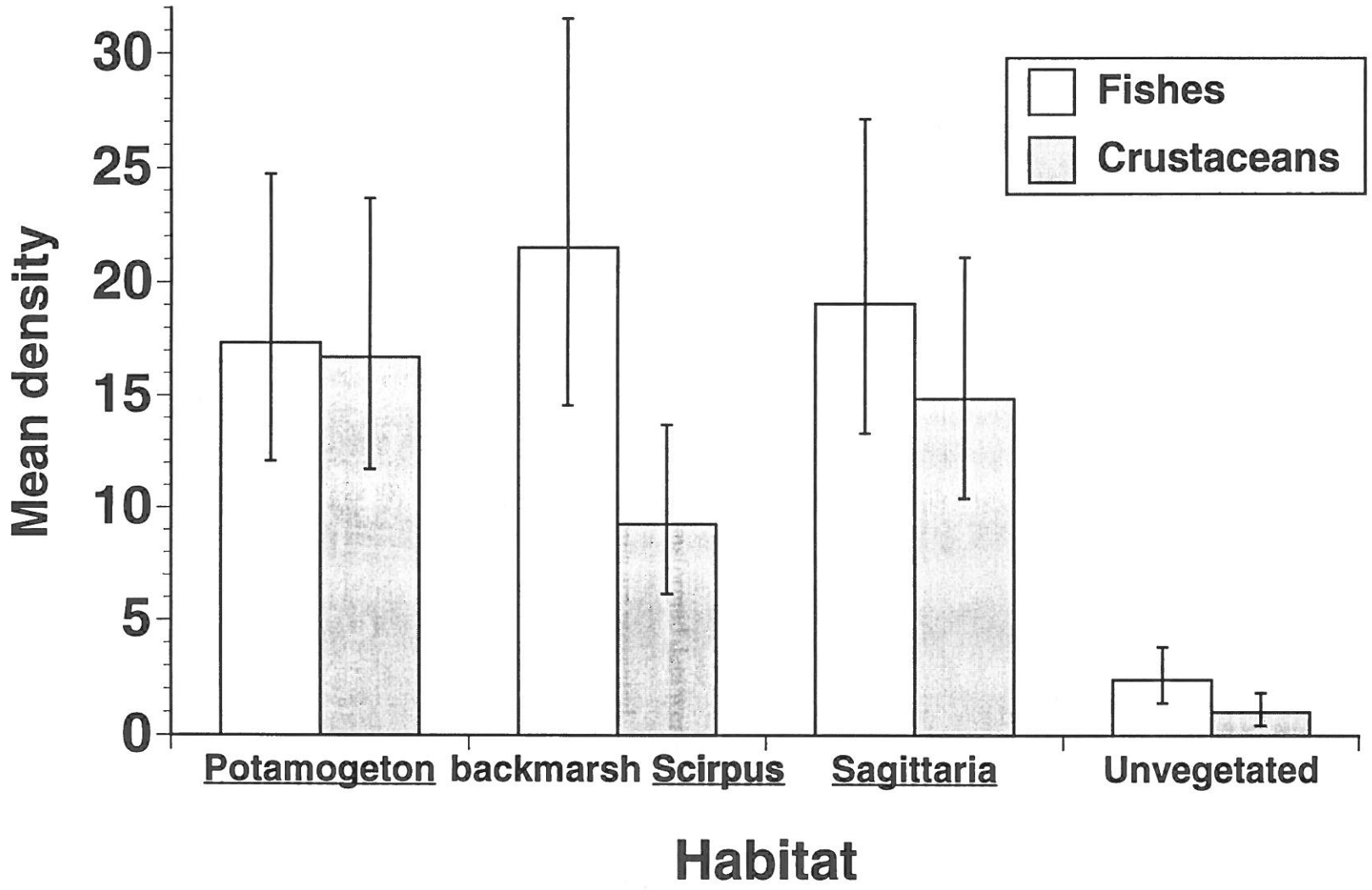

Mean density
30
25
20
15
10
5
0
Fishes
Crustaceans
Potamogeton
backmarsh
Scirpus
Sagittaria
Unvegetated
Habitat

Figure 1.3b Mean density (individuals/m^2) of sheepshead minnow Cyprinodon variegatus, rainwater Lucania parva, bay anchovy Anhcoa mitchilli, and inland silverside Menidia beryllina collected in fall 1994 from Potamogeton, backmarsh Scirpus, Sagittaria, and unvegetated habitats. Least Square Means and confidence limits of transformed data were calculated from 24 samples. Back-transformed means and confidence limits are presented. Error bars = 95% confidence interval.

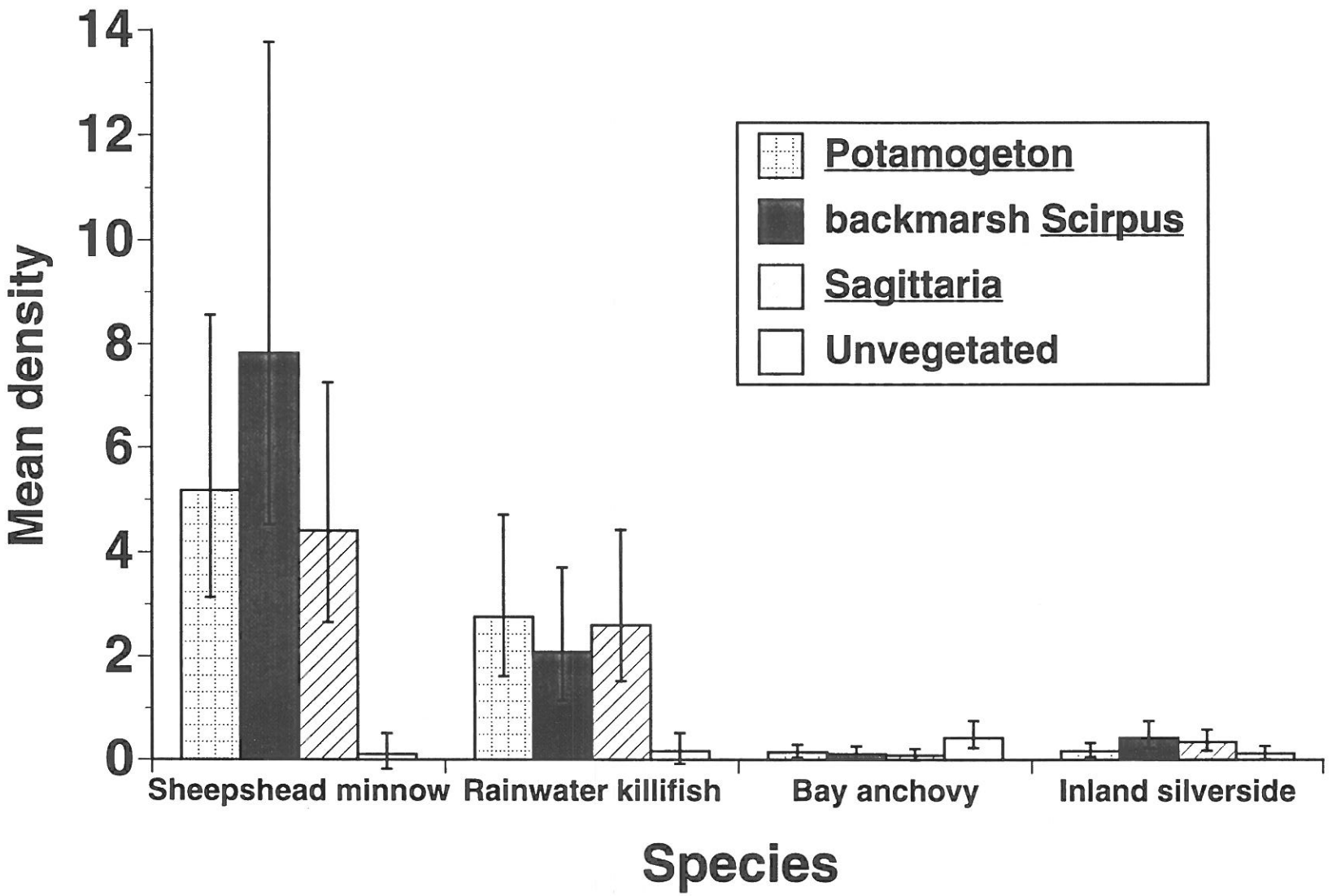
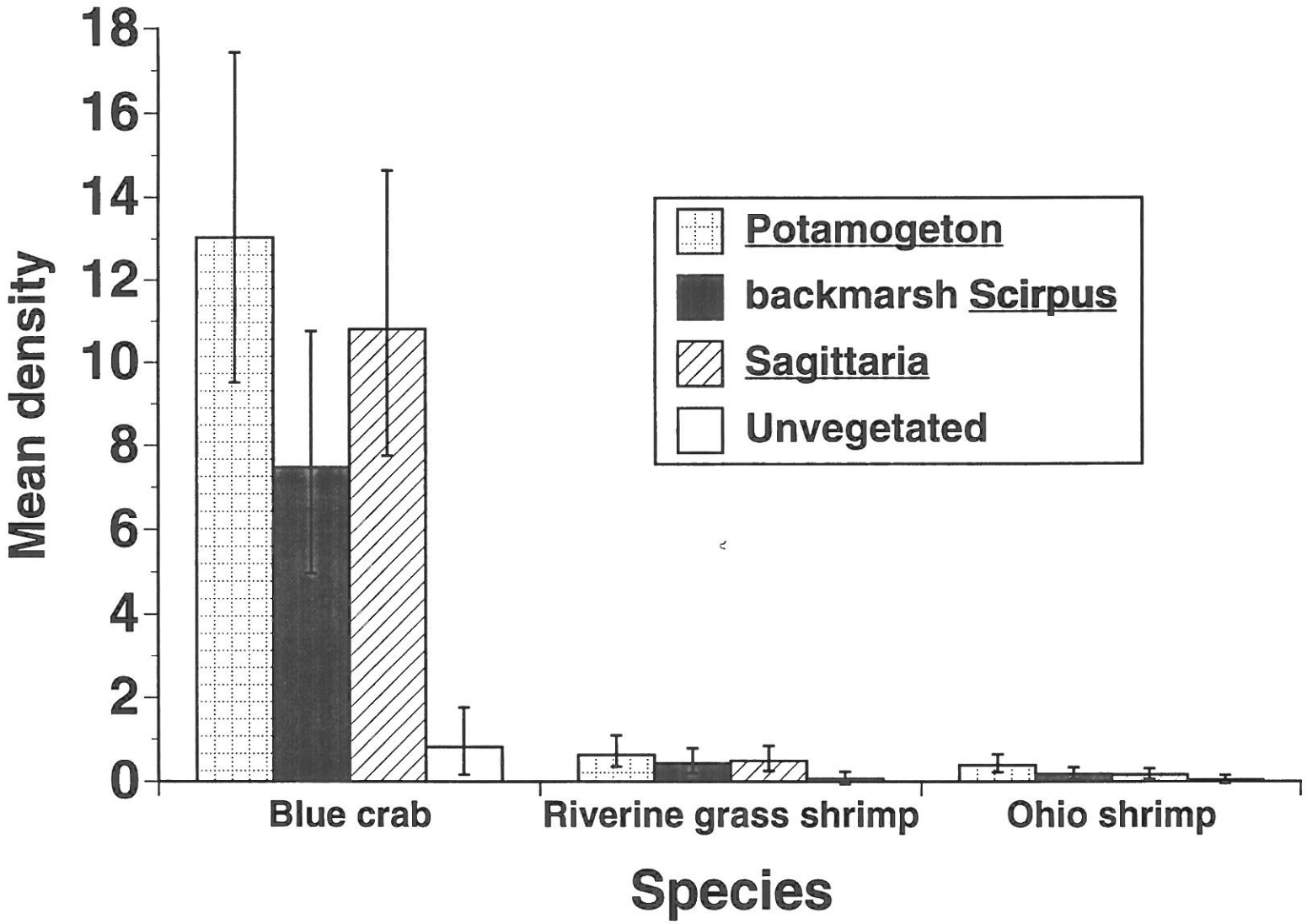

14
12
10
8
6
4
2
0
Mean density
Potamogeton
backmarsh Scirpus
Sagittaria
Unvegetated
Sheepshead minnow
Rainwater killifish
Bay anchovy
Inland silverside
Species

Figure 1.3c Mean density (individuals/m^2) of blue crab Callinectes sapidus, riverine grass shrimp Palaemonetes paludosus, and Ohio shrimp Macrobrachium ohione collected in fall 1994 from Potamogeton, backmarsh Scirpus, Sagittaria, and unvegetated habitats. Least Square Means and confidence limits of transformed data were calculated from 24 samples. Back-transformed means and confidence limits are presented. Error bars = 95% confidence interval.


Mean density
18
16
14
12
10
8
6
4
2
0
Potamogeton
backmarsh Scirpus
Sagittaria
Unvegetated
Blue crab
Riverine grass shrimp
Ohio shrimp
Species

but densities in Potamogeton, backmarsh Scirpus, and Sagittaria, were not significantly different (Fig. 1.3c, Table 1.3).

Habitat use: spring

By spring 1995, SAV and emergent vegetation had begun to recover from the previous winter die back and grazing by waterfowl. Large, dense patches of Potamogeton were established in the backmarsh and new stems of Scirpus occupied backmarsh and streamside areas of the study area. Patches of Najas, interspersed with an equal amount of unvegetated bottom, covered the intertidal and shallow subtidal areas of the study area where Potamogeton was absent.

During spring, numerically dominant fishes were bay anchovies, freshwater gobies, speckled worm eels Myrophis punctatus, and darter gobies Gobionellus boleosoma; together, these species accounted for >75% of the total fishes (Table 1.2). Densities of total fishes were significantly greater in Potamogeton than unvegetated habitat. Speckled worm eel densities were higher in Potamogeton than unvegetated bottom, and darter goby densities were higher in Najas than in unvegetated areas (Fig. 1.4a, Table 1.3). Densities of speckled worm eels were significantly greater in Potamogeton than backmarsh Scirpus, but densities in Potamogeton, Najas, and streamside Scirpus were not significantly different. Darter gobies were significantly more abundant in Najas than streamside Scirpus, but densities in Najas, Potamogeton, and backmarsh Scirpus were not significantly different. Mean densities of bay anchovies and freshwater gobies were not significantly different among habitats (Fig. 1.4b, Table 1.3).

As in summer and fall, Ohio shrimp, blue crabs, and riverine grass shrimp numerically dominated crustacean assemblages in spring, accounting for >99% of total catch (Table 1.2). Total crustacean and blue crab densities were significantly greater in Potamogeton than all other habitats (Figs. 4a and 4c, Table 1.3). Riverine grass shrimp were significantly more abundant in Potamogeton than Najas, but densities in Potamogeton, streamside Scirpus, and backmarsh

Figure 1.4a Mean density (individuals/m^2) of total fishes and total crustaceans collected in spring 1995 from Potamogeton, Najas, backmarsh Scirpus, streamside Scirpus, and unvegetated habitats. Least Square Means and confidence limits of transformed data were calculated from 12 samples for Najas and 24 samples for all other habitats. Back-transformed means and confidence limits are presented. Error bars = 95% confidence interval.

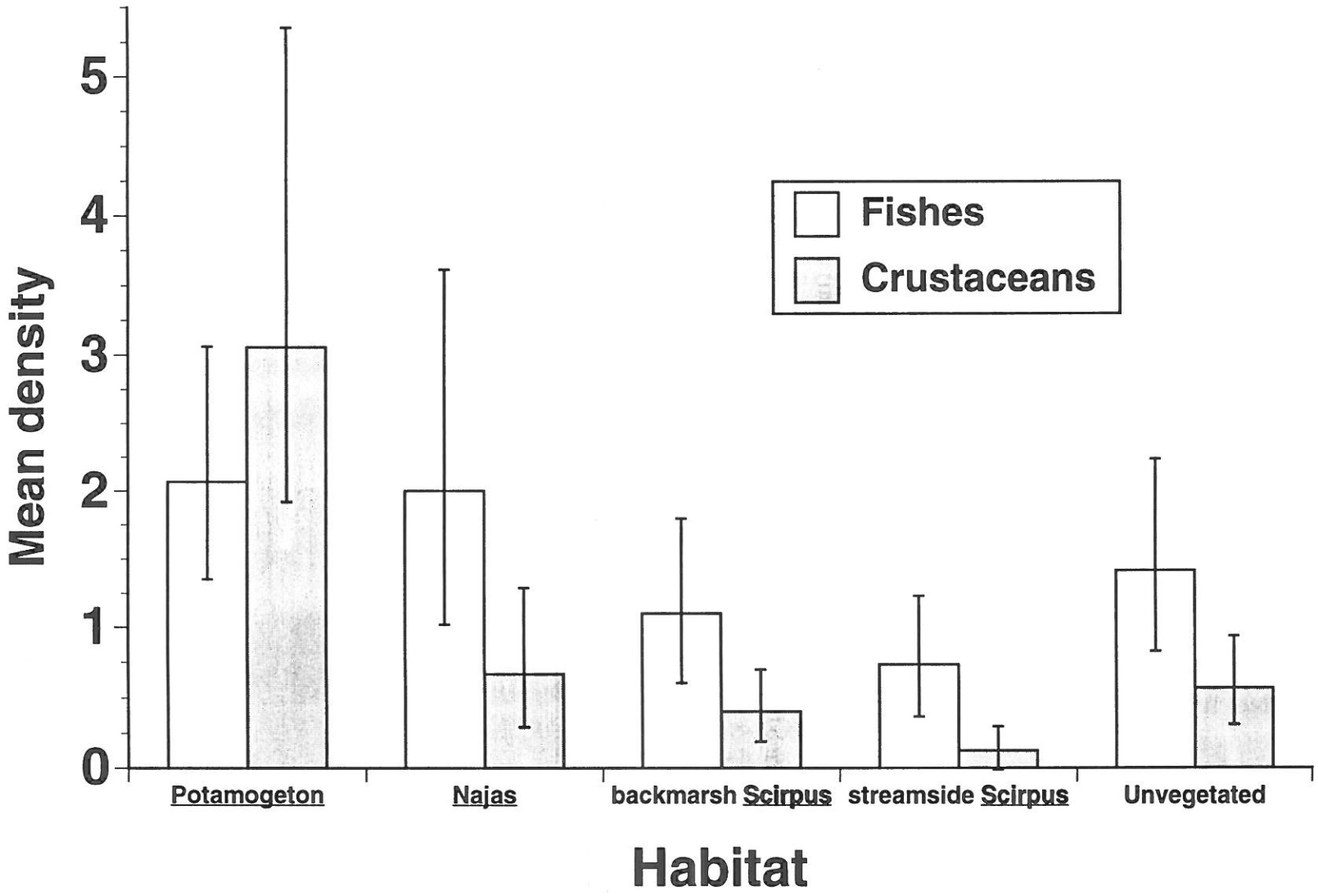

Mean density
0
1
2
3
4
5
Fishes
Crustaceans
Potamogeton
Najas
backmarsh Scirpus
streamside Scirpus
Unvegetated
Habitat

Figure 1.4b Mean density (individuals/m^2) of bay anchovy Anchoa mitchilli, freshwater goby Gobionellus shufeldti, speckled worm eel Myrophis punctatus, and darter goby Gobionellus boleosoma collected in spring 1995 from Potamogeton, Najas, backmarsh Scirpus, streamside Scirpus, and unvegetated habitats. Least Square Means and confidence limits of transformed data were calculated from 12 samples for Najas and 24 samples for all other habitats. Back-transformed means and confidence limits are presented. Error bars = 95% confidence interval.

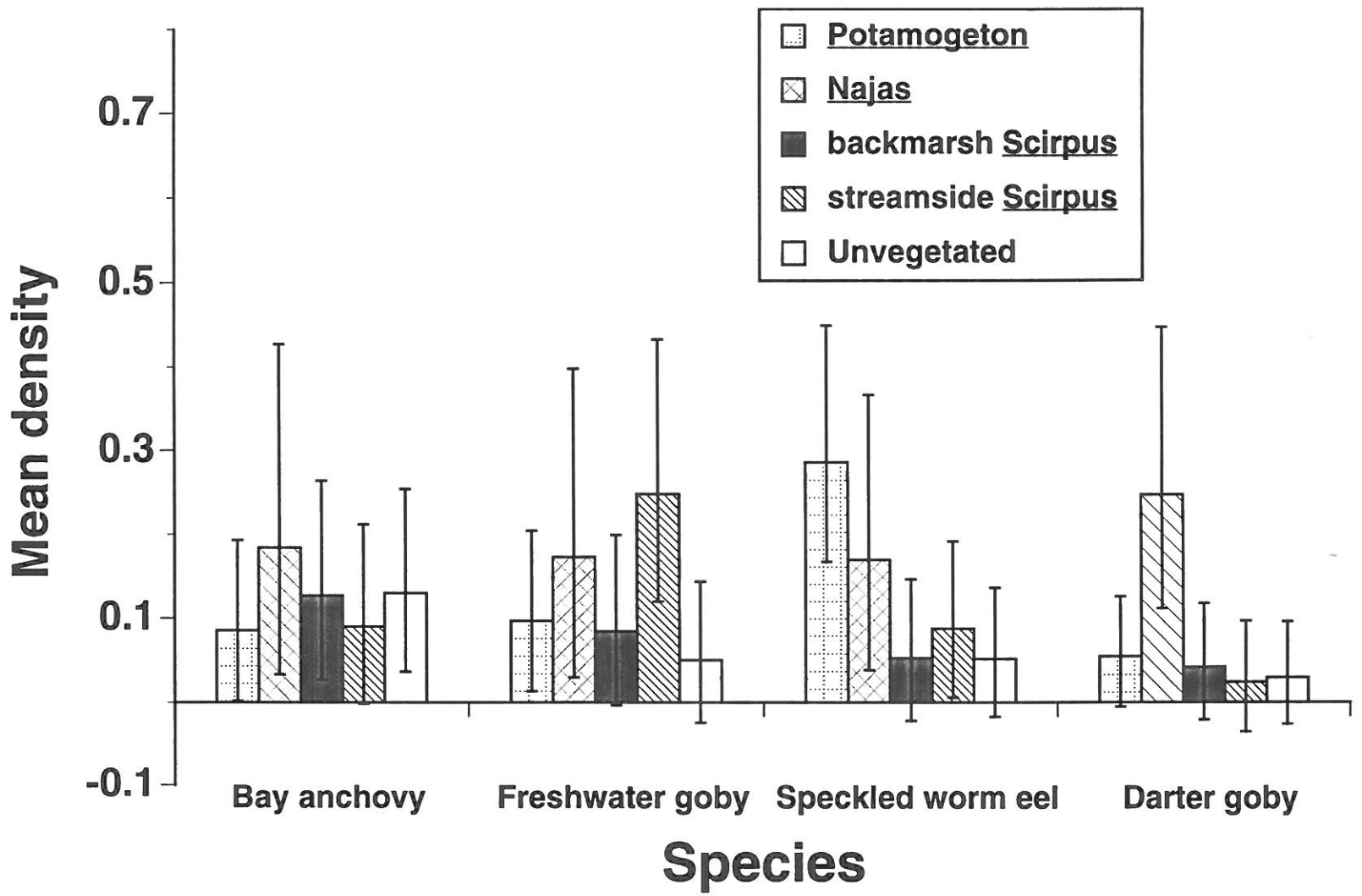
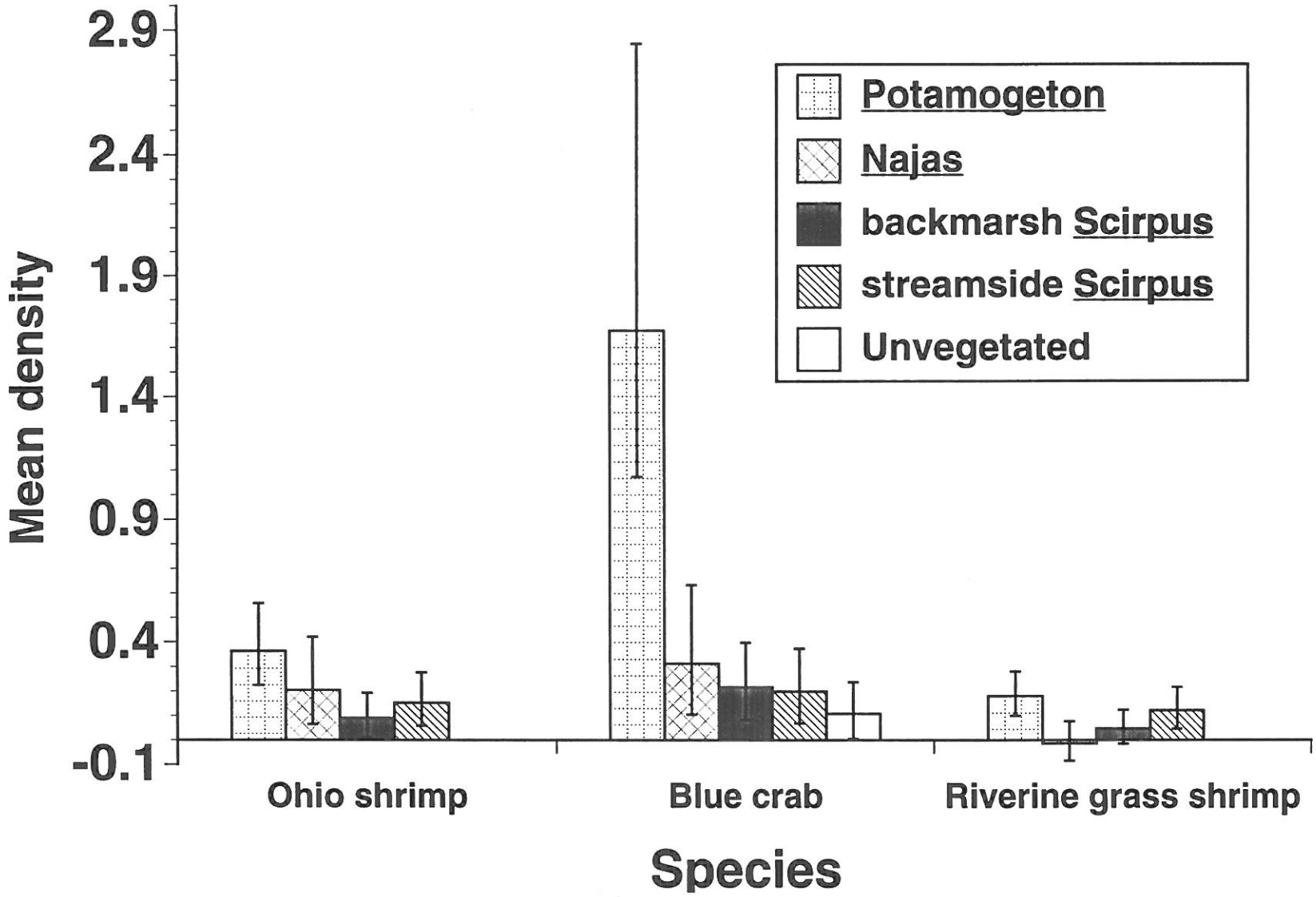

Potamogeton
Najas
backmarsh Scirpus
streamside Scirpus
Unvegetated
Mean density
0.7
0.5
0.3
0.1
-0.1
Bay anchovy
Freshwater goby
Speckled worm eel
Darter goby
Species

Figure 1.4c Mean density (individuals/m^2) of Ohio shrimp Macrobrachium ohione, blue crab Callinectes sapidus, and riverine grass shrimp Palaemonetes paludosus collected in spring 1995 from Potamogeton, Najas, backmarsh Scirpus, streamside Scirpus, and unvegetated habitats. Least Square Means and confidence limits of transformed data were calculated from 12 samples for Najas and 24 samples for all other habitats. Back-transformed means and confidence limits are presented. Error bars = 95% confidence interval.


2.9
2.4
1.9
1.4
0.9
0.4
-0.1
Mean density
Potamogeton
Najas
backmarsh Scirpus
streamside Scirpus
Unvegetated
Ohio shrimp
Blue crab
Riverine grass shrimp
Species

Scirpus were not significantly different (Fig. 1.4c, Table 1.3). Ohio shrimp were significantly more abundant in Potamogeton than backmarsh Scirpus, but densities in Potamogeton, Najas, and streamside Scirpus were not significantly different. Riverine grass shrimp and Ohio shrimp were not collected on unvegetated bottom.

Environmental parameters

Environmental parameters differed seasonally. Mean salinities and mean water depths were greatest in fall, whereas mean temperatures and mean vegetation biomasses were greatest in summer (Table 1.4).

Statistically significant differences among habitats also were found for most environmental parameters within each season. Mean parameter values (tested simultaneously) were significantly different among habitats in summer (Wilks' Lambda = 0.46, $F_{15,230} = 4.95$; $p<0.0001$), fall (Wilks' Lambda = 0.16, $F_{15,235} = 14.64$; $p<0.0001$), and spring (Wilks' Lambda = 0.05, $F_{20,319} = 22.31$; $p<0.0001$) (Table 1.5). Mean salinities, however, were not significantly different among habitats. In both seasons that streamside Scirpus was sampled (summer and spring) this habitat had significantly lower mean water temperatures than all other habitats (except Najas in summer). Substrate elevations (and mean water depths) in SAV and unvegetated habitats were not significantly different, but unvegetated bottom was significantly lower in elevation and flooded more deeply than emergent habitats (fall and spring, Tables 4 and 5). Mean water depths were significantly greater in SAV (Potamogeton and Najas) than streamside Scirpus in summer and greater in SAV than in either streamside or backmarsh Scirpus in spring. The substrate elevation of streamside Scirpus was significantly higher than that of all other habitats in fall. Streamside Scirpus had significantly more standing biomass than backmarsh Scirpus (summer and spring), whereas the standing biomass of backmarsh Scirpus was significantly greater than that of Sagittaria (fall). Mean vegetation biomass of

Table 1.4 Means with S.E. (one standard error), untransformed data, of environmental and vegetation (biomass) parameters for each habitat and season. Each mean was calculated from 24 samples except 22 samples for streamside Scirpus americanus, and 12 for Najas guadalupensis in Spring 1995. Means for salinity in summer and spring were within the accuracy range of the salinometer and therefore, they were not included in the statistical analyses. Results (P values) of MANOVA and ANOVA tests (considered significant at $p<0.05$) comparing mean measurements among habitats within a season are given for each parameter. Blank spaces represent seasons in which habitats were not dominant and therefore not sampled.

	Potamogeton nodosus		Najas gaudalupensis		Scirpus americanus backmarsh		Scirpus americanus streamside		Sagittaria spp.		Unvegetated		MANOVA Wilks' Lambda	ANOVA
Parameter	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	P value	P value
Summer 1994													0.0001	
Salinity (°/oo)	0.2	(0.01)	0.2	(0.01)	0.3	(0.01)	0.3	(0.01)						
Temperature(°C)	31.4	(0.42)	30.6	(0.64)	31.3	(0.44)	29.3	(0.28)						0.0030
Water depth (cm)	28.8	(1.76)	30.9	(1.98)	25.3	(1.29)	16.7	(0.96)						0.0001
Elevation (cm)	13.4	(1.89)	12.2	(1.87)	19.7	(1.05)	20.9	(1.60)						0.1242
Vegetation (g/m^2)	40.6	(5.15)	36.4	(6.59)	43.0	(7.79)	104.2	(14.11)						0.0001
Fall 1994													0.0001	
Salinity (°/oo)	1.3	(0.27)			1.7	(0.30)			1.0	(0.23)	1.4	(0.29)		0.1996
Temperature(°C)	27.9	(0.43)			27.4	(0.34)			26.8	(0.41)	27.3	(0.37)		0.0482
Water depth (cm)	41.0	(1.81)			37.8	(1.64)			35.9	(1.53)	43.6	(1.40)		0.0016
Elevation (cm)	2.9	(1.75)			9.6	(1.38)			6.1	(2.08)	1.6	(1.56)		0.0072
Vegetation (g/m^2)	21.9	(2.61)			72.2	(18.62)			27.1	(4.82)				0.0019
Spring 1995													0.0001	
Salinity (°/oo)	0.2	(0.01)	0.2	(0.01)	0.2	(0.01)	0.2	(0.00)			0.2	(0.01)		
Temperature(°C)	28.5	(0.35)	28.5	(0.31)	29.1	(0.42)	25.5	(0.11)			28.5	(0.40)		0.0001
Water depth (cm)	31.5	(1.82)	30.3	(1.10)	20.4	(1.32)	17.6	(1.17)			31.1	(2.06)		0.0001
Elevation (cm)	13.6	(1.60)	21.9	(1.40)	25.8	(1.65)	33.2	(1.40)			14.7	(1.68)		0.0001
Vegetation (g/m^2)	14.0	(1.18)	2.3	(0.43)	18.4	(3.88)	50.3	(10.36)						0.0001

Table 1.5 Results of Least Square Means comparison tests on significant ($p<0.05$) ANOVA test results of environmental parameters. Nonsignificant ANOVA tests are indicated by "NS". Habitats are listed in descending order of mean parameter values. Means that did not differ significantly at $p<0.0083$ ($p<0.005$ for spring) are joined by a line (---). Habitats are represented as follows: PN=Potamogeton nodosus, NG=Najas guadalupensis, BSA=Scirpus americanus (backmarsh), SSA=Scirpus americanus (streamside), SG=Sagittaria, and UN=unvegetated.

Parameter	Summer 1994	Fall 1994	Spring 1995
Salinity	NS	NS	NS
Water temperature	PN BSA NG SSA	PN BSA UN SG	NG BSA UN PN SSA
Water depth	NG PN BSA SSA	UN PN BSA SG	NG PN UN BSA SSA
Elevation	NS	BSA SG PN UN	SSA BSA NG UN PN
Vegetation biomass	SSA BSA PN NG	BSA SG PN	SSA BSA PN NG

Potamogeton was significantly greater than that of Najas in spring, but biomass means of the two SAV habitats were not significantly different in summer.

Although a few correlations between environmental variables were significant, correlations were not high enough to justify excluding or combining variables; therefore, all variables (except salinity in summer and spring) were used in tests for correlation with total fish density and total crustacean density. Salinity was not included in the correlation analysis for summer and spring, because salinities then were nearly the same throughout the study area. Significance levels for correlation analyses were adjusted to 0.00625 for summer and spring and 0.005 for fall using the Bonferroni method. In summer, total crustacean mean density was significantly positively correlated with water depth ($r = 0.32$) and significantly correlated with elevation ($r = -0.31$) (Table 1.6). During fall and spring, no statistically significant correlations were found between environmental parameters and animal densities.

Recovery efficiency

The first removal efficiency experiment using sheepshead minnow resulted in 100% and 99% mean recovery efficiencies in SAV and emergent vegetation, respectively (Table 1.7). I recovered 99% of the fish in SAV after only 3 net sweeps and 100% after 5 sweeps. In emergent vegetation, I recovered 98% of the fish after 5 net sweeps and 99% after 9 sweeps. I calculated mean removal efficiencies of 100% and 98% in SAV and emergent vegetation, respectively for experiments using Ohio shrimp as the test organism. Ninety-four percent of the shrimp in SAV were removed after only 3 sweeps of the net, and 100% were taken after 5 sweeps. In emergent vegetation, I recovered 93% of the shrimp after 3 net sweeps and 98% after 7 sweeps.

Flooding duration

Flooding durations were higher in spring and fall than in summer, and the difference in mean flooding duration among habitats was relatively consistent for months within a season

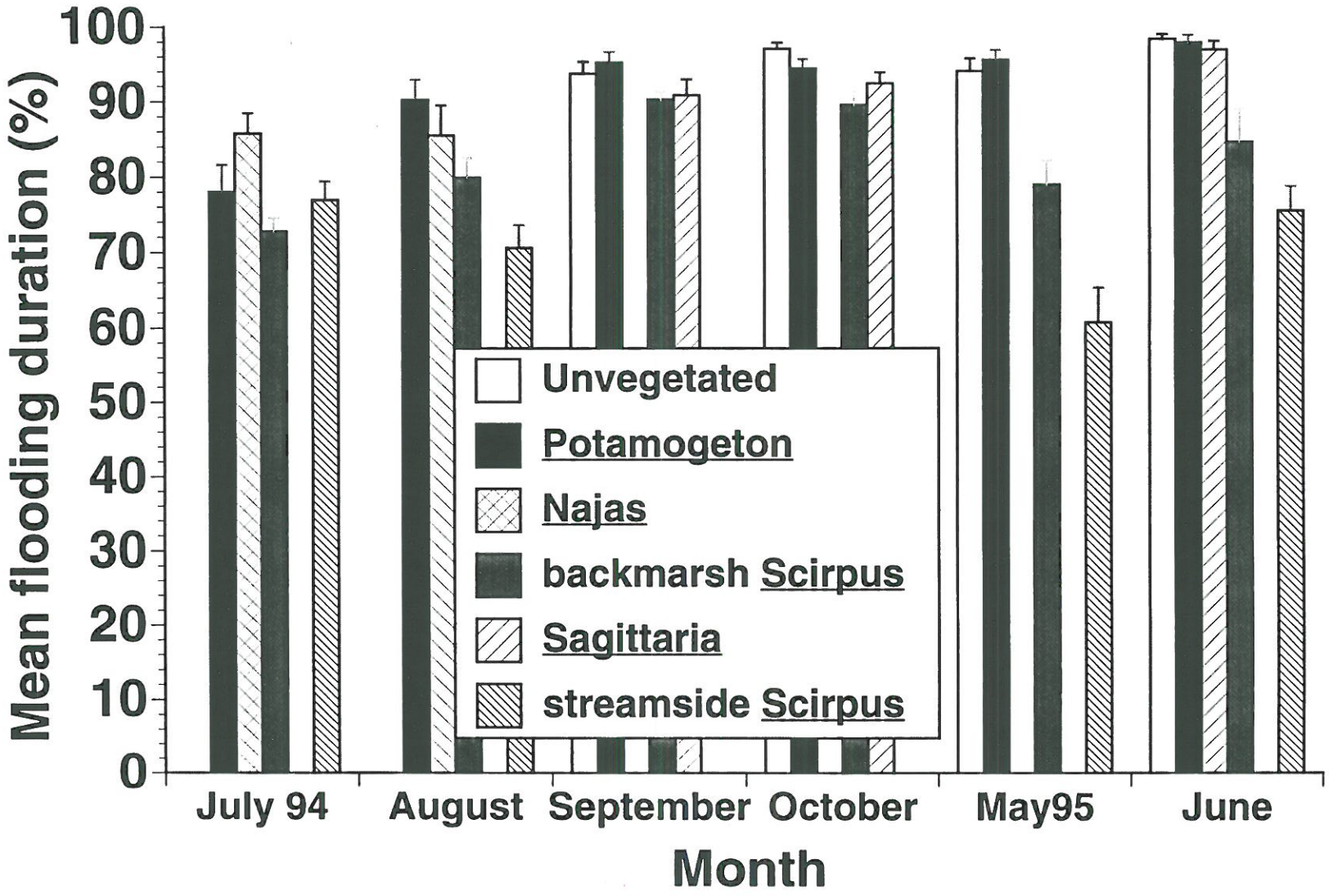
Table 1.6 Pearson correlation coefficients for environmental parameters and fish and crustacean densities (all data transformed) for all seasons. Coefficients that were considered significantly different from 0 (at $p<0.00625$ for summer and spring and at $p<0.005$ for fall), are indicated with an (*). Correlation coefficients for vegetation were computed from 72 samples in fall, 84 samples in spring, and 94 samples in summer. Correlation coefficients were computed for other variables from 94 samples in summer, 96 samples in fall and 108 samples in spring. Vegetation was characterized as sample biomass, dry weight (g/m^2). Blank spaces indicate that salinity was not used in the analysis for summer or spring because then salinities were nearly uniform throughout the study area.

	Summer		Fall		Spring	
Parameter	Total fish	Total crustaceans	Total fish	Total crustaceans	Total fish	Total crustaceans
Salinity			-0.22	0.27		
Water temperature	0.28	0.13	0.11	-0.13	-0.18	-0.03
Water depth	0.22	0.32*	-0.23	0.10	0.13	0.20
Elevation	-0.11	-0.31*	0.23	0.15	-0.04	-0.21
Vegetation	-0.13	0.02	0.31	0.32	-0.04	0.03

Table 1.7 Efficiency estimates for removing animals from the $1m^2$ throw trap using a 1x1 m bar seine. Habitat was either SAV (Potamogeton nodosus) or emergent vegetation (Scirpus americanus). Size range and mean (fish: standard length, shrimp: total length), number of tests (tests), number of organisms tested (total), and mean efficiency with one standard error (efficiency) are given for each species tested.

Species	Habitat	Size range (mean), mm	Tests	Total	Efficiency
Sheepshead minnow	SAV	20-39 (26)	10	100	1.00 ± 0.00
	Emergent	20-37 (26)	10	100	0.99 ± 0.03
Ohio shrimp	SAV	16-36 (26)	10	100	1.00 ± 0.00
	Emergent	20-38 (25)	10	100	0.98 ± 0.04

Figure 1.5 Estimated mean monthly flooding duration [(hours habitat inundated) / (total hours in month) x 100] for July 1994 through October 1994 and May and June 1995. Means and standard errors (S.E.) were calculated for 72 Potamogeton and backmarsh Scirpus sites, 48 streamside Scirpus and unvegetated sites, 36 Najas sites, and 24 Sagittaria sites. Error bars = 1 S.E.


Mean flooding duration (%)
100
90
80
70
60
50
40
30
20
10
0
July 94
August
September
October
May95
June
Month
Unvegetated
Potamogeton
Najas
backmarsh Scirpus
Sagittaria
streamside Scirpus

(Fig. 1.5). Submerged aquatic vegetation and unvegetated bottom had the highest flooding durations; in spring and fall when both habitats were sampled, SAV and unvegetated habitats were almost constantly flooded (>94%). In summer, SAV was flooded >75% of the time. Emergent vegetation was flooded for shorter periods than SAV and unvegetated bottom, but flooding durations for all emergent habitats (except streamside Scirpus) also were long (>70%). Except for July, streamside Scirpus had the shortest flooding durations of all habitats (61-77%).

DISCUSSION

Although densities of most nektonic species differed among shallow estuarine habitats of the Atchafalaya River Delta, a clear difference in habitat use between marsh edge and SAV was not observed for most species. Only three species showed an apparent habitat preference between marsh edge and SAV. Inland silversides and freshwater gobies were most abundant in Scirpus marsh in summer, whereas blue crabs were most abundant in SAV (Potamogeton) in spring. Direct comparisons of nekton populations between SAV and marsh are few. Two such studies were limited to blue crabs (Thomas et al. 1990; Heck et al. 1994); only one examined entire assemblages of nekton species (Rozas and Minello 1998). Thomas et al. (1990) found significantly greater densities of blue crabs in seagrass than saltmarsh for 7 of 12 months they sampled, but Heck et al. (1994) did not find consistent differences in average monthly crab densities between seagrass and saltmarsh. Numerically dominant fish and decapod crustacean densities were either significantly greater in marsh edge than seagrass, or no significant difference was found between the two habitats (except for brown shrimp Penaeus aztecus in May) in a study of a south Texas estuary (Rozas and Minello 1998). Although the tidal freshwater system I studied is floristically very different from the more saline system studied by Rozas and Minello (1998), my results are consistent with theirs in that densities of most species were similar in marsh edge habitat and SAV.

Dominant macrophytes of marsh and SAV habitats in my study area were morphologically very different. Potamogeton has relatively bare stems except for leaves located at their distal ends; these floating leaves form a thin, discontinuous layer of vegetation at the water surface. This layer, however, appears complete enough to obscure the view of avian predators, although I observed little avian predation of nektonic organisms in my study area. Najas has numerous small, densely-packed, submerged leaves. Scirpus and Sagittaria have slender, sometimes dense leaves that extend above the water surface. Vegetation morphology has been shown to influence habitat use by fishes and crustaceans in other studies (Heck and Orth 1980a; Stoner and Lewis 1985; Bell and Westoby 1986a; Chick and McIvor 1994), but it did not seem to influence nekton distribution in my study. Protection from predators was likely provided by both SAV and marsh vegetation (West and Williams 1986; Wilson et al. 1987; Rozas and Odum 1988; Minello 1993), and any differences in refuge value provided by SAV and emergent vegetation were apparently too little to influence habitat use.

Other factors that may affect nekton habitat use in SAV and marsh are elevation and vegetation structural complexity. At high tide, killifish show an apparent preference for the highest inundated saltmarsh available, whereas penaeid shrimp remain in low, deeply flooded marsh (Kneib 1984; Rozas and Reed 1993). In my study, backmarsh Scirpus marsh and SAV were similar in substrate elevation, and nekton densities differed little between these habitats. Rozas and Minello (1998) also found that densities of most nekton species did not differ between seagrass and marsh habitats; in their study, mean substrate elevations in marsh and seagrass differed by only 11 cm. This is similar to the 12 cm difference in mean substrate elevation that I observed between marsh and SAV in my study area. In contrast, Thomas et al. (1990) documented significantly higher densities of blue crabs in seagrass than Spartina marsh in most months they sampled. The difference in blue crab densities between marsh and SAV found by Thomas et al. (1990) may be partially attributed to the relatively large difference in substrate elevation (24 cm) between the habitats they sampled (Rozas and Minello 1998).

The presence of SAV may have increased the structural complexity of emergent habitats in my study area and thus may also have contributed to our finding few differences in nekton densities between vegetated habitats. At some marsh sample sites, Najas or other species of SAV grew among Scirpus and Sagittaria stems. It is possible that this added structure attracted additional animals to emergent vegetation, including species usually associated with SAV. Rozas and Minello (1998) also found aquatic vegetation (seagrass fragments) near Spartina stems at the marsh edge, and speculated about the possible habitat enhancement caused by this additional structure in marsh vegetation.

The presence of vegetation was apparently more important than the species or morphology of the existing vegetation in influencing nekton distribution among habitats. Vegetated habitats in the delta supported much higher densities of most nekton than unvegetated sites. My results are consistent with numerous other studies conducted in estuaries that show an apparent selection of marsh or submerged vegetation over unvegetated habitats by fish and crustaceans (Briggs and O'Connor 1971; Heck and Orth 1980b; Orth and Heck 1980; Zimmerman and Minello 1984; Rozas and Odum 1987a; Lubbers et al. 1990; Thomas et al. 1990; Williams et al. 1990; Sogard and Able 1991; Connolly 1994a; 1994b; West and King 1996). However, unlike most studies comparing SAV and unvegetated habitats in estuaries, presence of submerged vegetation was not confounded with water depth in my study. Substrate elevations and flooding depths were not significantly different in SAV and unvegetated bottom. Therefore, water depth could not have played a role in the apparent selection of vegetated habitats over unvegetated bottom that I found. Water depth may affect fish and crustacean distributions among estuarine habitats because predation rates may increase with water depth (McIvor and Odum 1988; Ruiz et al. 1993; Miltner et al. 1995). In studies comparing vegetated and unvegetated habitats, nekton and epifaunal densities are often positively correlated with vegetation biomass (Adams 1976; Heck and Wetstone 1977; Heck and Orth 1980b; Stoner 1983; Heck and Thoman 1984; Lubbers et al. 1990; Montague and Ley 1993); however, I found no such relationship.

Higher nekton densities in vegetated than unvegetated areas is often ascribed to greater protection and/or more food provided by vegetated habitats (Gilinsky 1984; Rozas and Odum 1988; Fredette et al. 1990; Lubbers et al. 1990; Minello 1993). Vegetation provides a refuge from predators , and experimental evidence suggests that at least some fish and crustacean species actively select protective vegetated habitats (Bell and Westoby 1986b). Artificial plant stems added to aquaria decreased predation of bluegill Lepomis macrochirus by largemouth bass Micropterus salmoides, but only after a threshold of 50 stems m^{-2} was reached (Savino and Stein 1982). When Atlantic croaker Micropogonias undulatus were allowed to feed on white shrimp Penaeus setiferus or brown shrimp in aquaria with artificial Spartina stems, Atlantic croaker consumed mostly white shrimp because few white shrimp used vegetation for cover (Minello and Zimmerman 1985). Palaemonid shrimp were preyed upon significantly less in vegetated than bare aquaria (Coen et al. 1981), and blue crabs in eelgrass Zostera marina suffered less predation compared to blue crabs on bare substrate (Heck and Thoman 1981; Wilson et al. 1987). In a tidal freshwater marsh, SAV provided predation protection for killifish (Rozas and Odum 1988).

Vegetation also supports greater standing crops of invertebrate prey organisms than unvegetated areas (Gerking 1962; Menzie 1980; Crowder and Cooper 1982; Lubbers et al. 1990; Connolly 1994b). Several studies indicate that some fish eat more or larger prey in vegetated compared to unvegetated habitats (Rozas and Odum 1988; Lubbers et al. 1990). Although the foraging efficiency of fish predators may decrease when vegetation stem density or biomass becomes too great (Van Dolah 1978; Stoner 1982), this reduced foraging efficiency may be more than offset by the higher overall prey densities in vegetated than unvegetated habitats (Rozas and Odum 1988). Prey densities may be insufficient in unvegetated substrate to support the high densities of nekton often found in vegetated habitats.

Backmarsh areas may provide more valuable habitat than streamside areas in the Atchafalaya Delta. Several species (sheepshead minnow, rainwater killifish, darter goby, and blue crab) were more abundant in at least one vegetated backmarsh habitat than streamside

Scirpus marsh. In contrast, only one species (freshwater goby) apparently selected streamside Scirpus over the backmarsh habitats. The shallow elevational gradient across the backmarsh may provide a refuge for nekton that is lacking along stream channels (McIvor and Odum 1988). Water has only to retreat a short distance from the streamside shoreline to force aquatic organisms into a deep channel where they may be more susceptible to predation (McIvor and Odum 1988; Ruiz et. al. 1993). In addition to the refuge provided by shallow water, extensive SAV beds adjacent to backmarsh Scirpus may also afford protection as the tide drops, and organisms are forced out of the marsh (Rozas and Odum 1987b); streamside Scirpus has little or no adjacent SAV. Other factors that may be important are water depth, vegetation density, and temperature. The water depth in inundated streamside Scirpus was generally lower than in flooded backmarsh habitats. Although some nekton species seek out the shallow marsh, others take advantage of deeply-flooded habitats with low substrate elevations because longer hydroperiods of these habitats offer longer periods of use (Rozas and Reed 1993). As with Spartina alterniflora (Linthurst and Seneca 1980), vegetation biomass and stem density of Scirpus increased with elevation and were highest in streamside Scirpus. Streamside Scirpus may be less desirable habitat if dense stems impede nekton movement in this habitat. Water temperatures were lower in streamside Scirpus than backmarsh habitat due to the proximity of streamside marsh to the river channel (Hoese 1976); however, the small range in mean temperature within a season between habitats makes it unlikely that temperature was important in affecting habitat use.

Direct comparisons between my study and other investigations of similar habitats are difficult, because few studies of nekton use of low-salinity habitats have employed quantitative sampling methods. However, two such studies collected quantitative samples and reported nekton densities from vegetated habitats. Rozas and Odum (1987a) used a 1 m^2 throw trap to sample submerged plant beds in tidal freshwater channels in Virginia, and Zimmerman et al. (1990) sampled marsh and SAV at oligohaline sites in the Trinity River Delta, Texas using a 2.6 m^2 drop sampler. Palaemonid shrimps and blue crabs were the most abundant crustaceans

collected in my study as well as these studies in Virginia and Texas. In samples from vegetated habitats, blue crabs were generally less abundant (overall = 0.45 m^{-2}) in Rozas and Odum's (1987a) study and similar in abundance in the Zimmerman et al. (1990) study to the densities I found in my study (0.1 - 4.9 m^{-2}). However, the high densities (up to 17 m^{-2}) of blue crabs that I documented in fall were not reported by Zimmerman et al. (1990). Daggerblade grass shrimp Palaemonetes pugio densities varied seasonally and ranged from 0 - 26 m^{-2} and 0 - 400 m^{-2} in the studies of Zimmerman et al. (1990) and Rozas and Odum (1987a), respectively. The only palaemonid shrimp collected in my study, riverine grass shrimp, was taken in densities ranging from 0 - 8 m^{-2}. In all three studies, most fishes taken in samples were from the cyrprinodontidae family. Densities of total fishes were consistently higher in the Rozas and Odum (1987a) study (50 - 150 m^{-2} for most months) than total fish densities reported by Zimmerman et al. (1990) (0.69 - 13 m^{-2}) and my study (1.5 - 30.5 m^{-2}). The timing of sample collections may have contributed to the higher densities of grass shrimp and fishes reported from the Virginia study; in the study, submerged vegetation was sampled at low tide when animals were concentrated in subtidal marsh channels (Rozas and Odum 1987a).

Nekton assemblages of the shallow estuarine habitats in my study area were dominated by small resident species of little direct economic value. However, blue crab, an important fishery species, was abundant in the study area in all seasons. Blue crabs were most numerous as small juveniles in vegetated habitats in fall. Densities in my study area were high (up to 17 crabs m^{-2}) and comparable to values reported from more saline regions of Gulf coast estuaries. Williams et al. (1990) reported blue crab densities as high as 14.4 m^{-2} in seagrass along the Alabama Gulf coast. Zimmerman and Minello (1984) documented blue crab densities in a Texas saltmarsh of 22.3 m^{-2} in November, but densities at other times of the year ranged from 2.6-15.0 m^{-2}. Thomas et al. (1990) found juvenile blue crab densities of up to 50.6 m^{-2} in a Texas seagrass bed, and up to 22.1 m^{-2} in Spartina marsh. Blue crabs were a more important component of the decapod crustacean assemblage in my study than in other studies of tidal freshwater systems where large numbers of daggerblade grass shrimp overshadowed other

crustaceans (Rozas and Odum 1987a, 1987c). The peak abundance of blue crabs I observed in fall reflects earlier recruitment of small juveniles to shallow estuarine nursery areas (Herke and Rogers 1984; Williams et al. 1990). The Atchafalaya Delta may be an important nursery area for blue crabs on the Louisiana coast.

Although sciaenids are often abundant in Gulf coast and Atlantic coast estuaries (Weinstein 1979; Baltz 1993), I collected only three individuals and species (Atlantic croaker Micropogonias undulatus, Spot Leiostomus xanthrus, and one unidentified drum). Other studies conducted in tidal freshwater marsh have similarly reported few or no sciaenids (Rozas and Odum 1987a; 1987b); however, Thompson and Deegan (1983) collected large numbers of juvenile sciaenids by seining in the Atchafalaya Delta. Their samples were likely taken from channels where I also collected several juvenile sciaenids using a bait seine (unpublished data). Young drum may seldom venture very far onto the shallow marsh; rather, they remain in deeper water near the marsh-channel interface (Baltz et al. 1993; Peterson and Turner 1994). Even though few commercially or recreationally important fish species occurred in the habitats I sampled, the high abundance of resident species found there may provide food for larger, economically important predatory fishes (Darnell 1961; Hoese 1976).

The emerging Atchafalaya Delta contains important habitat for nekton. Submerged grass beds and marsh edge appear to be equally important habitat for fishes and crustaceans in the Delta. Consistent with much of the literature, most nekton species used vegetated over unvegetated habitats. Also, most nekton appeared to prefer backmarsh habitats over streamside marsh along channels. High densities of juvenile blue crabs in emergent vegetation and submerged grass beds are an indication of the important nursery function of vegetated habitats in the Delta.

CHAPTER 2

INTRODUCTION

Shallow estuarine habitats are important for nekton species, especially as nursery areas (Weinstein 1979; Heck and Thoman 1984; Rozas and Hackney 1984; Orth and van Montfrans 1987). Given several available habitats, nekton often show an apparent preference for a particular type (Zimmerman and Minello 1984; Lubbers et al. 1990; Connolly 1994a; Rozas and Minello 1998). One factor thought to affect habitat choice for fish predators is differential foraging success.

The density of potential invertebrate prey for predatory fish often varies among habitats; and generally, vegetated habitats support greater numbers of invertebrate prey than unvegetated areas (Gerking 1962; Menzie 1980; Lubbers et al. 1990; Connolly 1994b). Invertebrate prey biomass is often positively correlated with submerged macrophyte density (Crowder and Cooper 1982). Therefore, shallow vegetated habitats often provide more prey for predatory fishes than unvegetated habitats, and high densities of fish predators usually coincide with these high prey densities in vegetated habitats (Rozas and Odum 1988; Lubbers et al. 1990).

In a previous study of a tidal freshwater system, I found that fish and decapod crustacean densities were significantly higher in vegetated than unvegetated habitats and at least three species (inland silverside, freshwater goby, and blue crab) exhibited an apparent habitat preference for a specific vegetated habitat (Chapter 1). A possible explanation for this apparent habitat selection is that organisms were responding to differences in food resources among habitats. If nekton predators choose habitat because of food value, and prey are distributed nonrandomly among habitats, predator distributions may reflect prey distributions.

The objective of my study was to address the question: Is habitat use by fish predators influenced by the distribution of their prey? To address this question, I tested the null hypothesis that prey of small resident fishes in my tidal freshwater study area are equally abundant and consumed in equal numbers and volume in SAV, marsh, and over unvegetated bottom.

MATERIALS AND METHODS

Study Area

The study area within the Atchafalaya River Delta is located approximately 32 km south of Morgan City, Louisiana near latitude 29^0 N and longitude 91^0 W (Fig. 1.1, Chapter 1). Salinities in Atchafalaya Bay are below 0.5 ppt during most of the year (Orlando et al. 1993). Tides are predominantly diurnal and have a mean range of 0.2 m (U. S. Department of Commerce 1993). Water temperatures in Atchafalaya Bay are above 25^0C from May through September.

I conducted experiments at sites on Rodney Island, a natural island located east of East Pass (Fig. 1.1, Chapter 1). Vegetation on the island was diverse but submerged aquatic vegetation was dominated by Potamogeton nodosus and Najas guadalupensis. Emergent vegetation was dominated by Scirpus americanus, and additionally by Sagittaria platyphylla and Sagittaria latifolia in the fall. Sparse stands of Sagittaria platyphylla occurred in the low intertidal; this species was replaced by Sagittaria latifolia at slightly higher elevations. Thick, monospecific stands of Scirpus americanus occupied the highest intertidal areas.

Methods

I used foraging experiments to test the null hypothesis that food resources are the same in emergent vegetation, SAV, and unvegetated bottom (McIvor and Odum 1988; Rozas and Odum 1988). Two predatory fishes that were important members of the nekton assemblage in my study area were used in experiments conducted in October (gulf killifish Fundulus grandis) and in June (freshwater goby Gobionellus shufeldti).

Fish were collected with a seine and held overnight in aerated, insulated containers. Experiments were conducted within fifteen 1 m^2 circular enclosures made of 0.64-cm mesh hardware cloth connected to a wooden stake. At five sites, I haphazardly placed a 61 cm tall

enclosure in each of three habitats: SAV (Potamogeton nodosus), marsh (Scirpus americanus in June and Sagittaria spp. in October) and unvegetated bottom. I used the dominant emergent macrophyte in the study area at the time each experiment was conducted (Chapter 1). Enclosures were placed at least 2 m apart, and cage walls were pushed 10 cm into the sediment to prevent escape. Test fish were fin-clipped (i.e., anal fin removed) for later identification. At the beginning of each experiment, fish were added to each enclosure at a density (three per enclosure) approximately equal to that in natural habitats (Chapter 1). Fish were allowed to forage for 3 h and retrieved. I removed fish with dip nets or with a throw trap and bar seine. After animals were euthanized (put on ice), they were fixed in 15% formalin for at least 72 h, rinsed for at least 24 h, and transferred to 70% ethanol.

Retrieved fish were later measured ($\pm$ 1 mm) and weighed ($\pm$ 0.1 g), and the contents of their guts examined. I removed the part of the digestive tract from the esophagus to the second 180^0 bend of the intestine and examined contents under a dissecting microscope; organisms (prey) were identified to the lowest taxon possible. Prey were enumerated and the volume of each prey species was estimated. Prey items were flattened to a thickness of 1 mm on a microscope slide, the slide was placed over a piece of 1 mm^2 graph paper, and the area was estimated for each; the area was then converted to volume, mm^3 (Hellawell and Abel 1971). I compared mean numbers and mean volumes of total prey and of numerically dominant prey taxa among habitats using a 2-way ANOVA with habitat as the treatment effect and site as a blocking factor.

I collected samples of benthic and epiphytic fauna in the immediate area around enclosures after the enclosures were set in place, and before initiation of experiments. Using a 5-cm diameter plastic pipe (area = 20 cm^2), I took three 5-cm deep sediment cores at random locations around the outside of enclosures to sample benthic fauna at each cage site. Epiphytic fauna also was randomly sampled at these same locations at each vegetated cage site by clipping the vegetation at the substratum within a 625 cm^2 quadrat; clipped vegetation was removed and carefully placed into plastic bags. Benthic and epiphytic samples were fixed in

10% formalin stained with Rose Bengal for at least 48 h, then rinsed and transferred to 70% ethanol. Benthic samples were sieved (mesh size 0.5 mm) to remove animals. Vegetation from epiphytic samples was thoroughly rinsed over a 0.5 mm sieve to collect animals, and animals from both benthic and epiphytic samples were identified and counted. To test the null hypothesis that mean animal densities were not different among marsh, SAV, and unvegetated bottom, I compared total animal mean densities and mean densities of numerically dominant prey taxa from combined benthic and epiphytic samples among habitats using a 2-way ANOVA. All data were normalized to animals per 20 cm^2 prior to analyses. Habitat was the main effect and site was a blocking factor in the ANOVA model.

Feeding preferences among habitats and among prey taxa were determined for gulf killifish and freshwater goby using the linear index of food selection (Strauss 1979),

$$Li = ri - pi$$

where ri and pi are the relative abundances of prey item i in the gut and habitat, respectively. The index ranges from -1 to +1, with positive values indicating preference and negative values indicating avoidance or inaccessibility. I compared mean selection indices for each prey taxa among habitats using a 2-way ANOVA with habitat as the treatment effect and site as a blocking factor. Mean selection indices for all habitats combined were compared among numerically dominant prey taxa using a 2-way ANOVA with taxa as the treatment effect and site as a blocking factor.

Site was not significant in all habitat comparison tests of animal distributions, gut contents, and prey selectivity; therefore, site was included in the error term (Snedecor and Cochran 1967). Significance levels for ANOVA tests were adjusted from 0.05 using the sequential Bonferroni method described by Rice (1989). All significant ANOVA tests (indicated by an asterisk in tables) were followed by Tukey's (HSD) test of all pairwise comparisons. All statistical analyses were performed using SAS (SAS Institute 1989).

RESULTS

In 218 total epiphytic, benthic, and gut samples, I collected 49 taxa in 5 phyla (Table 2.1). Samples were numerically dominated by chironomids (1237), tubificid worms (1225), ostracods (920), and amphipods (467), which together accounted for 80% of all animals taken. I collected more benthic fauna in October (1464) than June (467), but epiphytic fauna were more abundant in June (1399) than in October (521).

Animal distributions

Tubificids, chironomids, Gammarus nr. mucronatus, and nematodes were numerically dominant and accounted for >84% of all fauna in October (Table 2.2). Tubificids, chironomids, and nematodes accounted for >94% of benthic fauna, whereas chironomids, Gammarus nr. mucronatus, Paranais sp., Neretina usnea, and Mytiliopsis leucophaeta represented >72% of epiphytic fauna. Mean densities of total animals (epiphytic and benthic fauna) and mean densities of taxa that were numerically dominant in gulf killifish guts were not significantly different among habitats (Fig. 2.1a; Table 2.2).

Chironomid larva, Gammarus nr. mucronatus, tubificids, nematodes and chironomid pupa were numerically dominant and accounted for >72% of the total fauna in June (Table 2.2). Tubificids, chironomid larvae, and nematodes dominated benthic samples and accounted for >82% of organisms collected. Chironomid larvae and Gammarus nr. mucronatus accounted for >57% of fauna in epiphytic samples. Mean densities of total animals (epiphytic and benthic fauna) and mean densities of chironomid larva (a numerically dominant prey species in freshwater goby guts) were significantly different among habitats (Fig. 2.1b; Table 2.2). Total animal densities were significantly greater in vegetated habitats than unvegetated bottom. Chironomid larva were significantly more abundant in Scirpus marsh than on unvegetated bottom, but mean densities of chironomid larva in Scirpus and unvegetated habitats were not significantly different from those in Potamogeton nodosus (Fig. 2.1b).

Table 2.1 List of taxa collected in epiphytic, benthic, and gut samples. Total number of animals collected (all samples combined) and the type of sample (B=benthic, E=epiphytic, G=gut) are given for each taxa. Where applicable, life stages (l=larval, p=pupa, a=adult) are indicated.

Taxon	Total number	Sample
Phylum Nematoda	262	B,E,G
Phylum Nemertea	2	E
Phylum Annelida		
Class Oligochaeta		
Family Tubificidae	1225	B,E
Family Naididae		
Paranais sp.	52	B,E
Class Hirudinea	4	E
Class Polychaeta		
Laeonereis culveri	1	B
Phylum Arthropoda		
Subphylum Uniramia		
Class Insecta		
Order Diptera		
Family Chiromomidae	1237 l,p	B,E,G
Family Ceratopogonidae	33 l,p	B,E
Family Ephydridae		
Hydrellia sp.	36 l,p	B,E
Order Ephemeroptera		
Family Caenidae	56 l	B,E
Family Baetidae	56 l	B,E
Order Hemiptera		
Family Corixidae	27	B,E,G
Order Trichoptera		
Species A	40 l,p	E
Species B	3 l	B,E
Species C	5 l,p	E
Order Odonata		
Family Coenagrionidae	44 l	B,E
Order Coleoptera		
Family Hydrophilidae		
Berosus sp.	3 l	E
Order Lepidoptera		
Species A	8 l	E
Species X	106 l,p	E
Order Hymenoptera		
Hydrellia sp. parasite	10 l,p	B,E
unidentified ant	2 a	E
unidentified insect	4 l,a	E,G

Table 2.1. (continued)

Taxon	Total number	Sample
Subphylum Cheliceriformes		
Class Chelicerata		
Subclass Arachnida		
Order Acarina		
unidentified mite	2	E
Order Aranae		
Unidentified spider	3	E
Family Salticidae	1	B
Subphylum Crustacea		
Class Maxillopoda		
Subclass Ostracoda		
Species A	907	B,E,G
Species B	1	E
Species C	12	G
Subclass Copepoda	41	E,G
Class Malacostraca		
Order Isopoda		
Species A	2	B,E
Lirceus sp.	2	E
Munna reynoldsi	20	B,E
Order Amphipoda		
Gammarus nr. mucronatus	421	B,E,G
Hyalella azteca	43	B,E
Species A	1	E
Species B	1	E
Species C	1	B
Order Decapoda		
Macrobrachium ohione	1	B
Order Mysidacea		
Taphromysis sp.	2	B
Class Branchiopoda		
Order Cladocera	5	E,G
unidentified crustacean	1	E
Phylum Mollusca		
Class Pelecypoda		
Mytiliopsis leucophyta	23	B,E
Rangia sp.	6	B,E
Class Gastropoda		
Neretina usnea	46	B,E
Littoridinops palustris	12	E
Family Ancylidae	17	B,E
Species C	7	B,E
Species D	15	B,E
Species E	2	E
Total	1595	

Table 2.2 Mean density of benthic and epiphytic fauna (number per 20 cm^2) with S.E. (one standard error) taken in each habitat sampled during each experiment. Results (P values) of ANOVA tests comparing mean densities of combined benthic and epiphytic samples among the three habitats are given for total animals and species that were numerically dominant in fish guts. The total catch (total number of animals collected in all habitats combined) is also listed. Each mean for a habitat was calculated from five replicate samples, and each of these habitat replicates was the mean of three core (benthic) or three quadrat (epiphytic) samples. Relative abundance (RA) is given for those species with at least 1% relative abundance. Life stage is indicated by l= larval, p=pupa, and a=adult. Blank spaces represent month in which habitat was not sampled.

	Potamogeton nodosus				Sagittaria				Scirpus americanus				Unvegetated				
	Benthic		Epiphytic		Benthic		Epiphytic		Benthic		Epiphytic		Benthic				
Taxa	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Total	RA%	P value
October 1994																	
Tubificidae	29.1	(3.96)	0.0	(0.01)	18.3	(2.44)	0.0	(0.00)					21.8	(4.57)	1049	52.8	
Chironomidae l	6.7	(2.05)	0.2	(0.04)	3.9	(0.56)	0.1	(0.03)					4.5	(0.66)	377	19.0	0.2619
Gammarus nr. mucronatus	0.7	(0.31)	0.2	(0.05)	0.3	(0.26)	0.1	(0.04)					0.0	(0.00)	131	6.6	0.0608
Nematoda	4.0	(2.71)	0.0	(0.00)	3.1	(1.16)	0.0	(0.00)					0.4	(0.27)	125	6.3	
Ostracoda sp. A	0.9	(0.27)	0.0	(0.02)	1.0	(0.35)	0.0	(0.01)					0.4	(0.32)	53	2.7	0.3476
Paranais sp.	0.1	(0.07)	0.1	(0.02)	0.0	(0.00)	0.0	(0.01)					0.0	(0.00)	52	2.6	
Neretina usnea	0.0	(0.00)	0.0	(0.01)	0.0	(0.00)	0.1	(0.02)					0.1	(0.07)	40	2.0	
Mytiliopsis leucophaeta	0.0	(0.00)	0.0	(0.01)	0.1	(0.08)	0.0	(0.00)					0.0	(0.00)	23	1.2	
Chironomidae p,a	0.1	(0.07)	0.0	(0.01)	0.2	(0.08)	0.0	(0.01)					0.1	(0.07)	21	1.1	
Hydrellia sp. p	0.0	(0.00)	0.0	(0.01)	0.0	(0.00)	0.0	(0.01)					0.0	(0.00)	12		
Coenagrionidae	0.3	(0.33)	0.0	(0.00)	0.2	(0.20)	0.0	(0.01)					0.1	(0.07)	12		
Munna reynoldsi	0.0	(0.00)	0.0	(0.00)	0.2	(0.08)	0.0	(0.01)					0.0	(0.00)	11		
Hyalella azteca	0.1	(0.07)	0.0	(0.00)	0.1	(0.07)	0.0	(0.01)					0.0	(0.00)	10		
Hydrellia sp. l	0.2	(0.13)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	10		
Ceratopogonidae l	0.3	(0.33)	0.0	(0.00)	0.2	(0.20)	0.0	(0.00)					0.1	(0.07)	9		
Hymenoptera parasite	0.1	(0.08)	0.0	(0.01)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	8		
Lepidoptera sp. A l	0.0	(0.00)	0.0	(0.01)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	6		
Hirudinida	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.01)					0.0	(0.00)	4		
Gastropoda sp. D	0.0	(0.00)	0.0	(0.00)	0.1	(0.07)	0.0	(0.00)					0.0	(0.00)	3		
Caenidae	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.1	(0.07)	3		
Spider	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	3		
Corixidae	0.1	(0.07)	0.0	(0.00)	0.1	(0.13)	0.0	(0.00)					0.0	(0.00)	3		
Isopoda sp. A	0.0	(0.00)	0.0	(0.00)	0.1	(0.07)	0.0	(0.00)					0.0	(0.00)	2		
Berosus sp.	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	2		
Acarina sp. A	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	2		
Nemertea	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	2		
Taphromysis sp.	0.0	(0.00)	0.0	(0.00)	0.1	(0.07)	0.0	(0.00)					0.1	(0.07)	2		
Gastropoda sp. C	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	1		
Littoridinops palustris	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	1		
Ant	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	1		
Lepidoptera sp. X l	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	1		
Lirceus sp.	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	1		
Ancylidae	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	1		
Trichoptera sp. C l	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	1		
Trichoptera sp. A l	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	1		
Amphipoda sp. A	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	1		
Amphipoda sp. B	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	1		
TOTAL ANIMALS	42.4	(5.04)	0.7	(0.13)	27.8	(1.96)	0.4	(0.08)					27.4	(5.10)	1985		0.0414

Table 2.2 (Continued)

	Potamogeton nodosus				Sagittaria				Scirpus americanus				Unvegetated				
	Benthic		Epiphytic		Benthic		Epiphytic		Benthic		Epiphytic		Benthic				
Taxa	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Total	RA%	P value
June 1995																	
Chironomidae I	2.3	(0.60)	0.5	(0.07)					3.8	(0.54)	0.7	(0.13)	1.8	(0.13)	680	36.4	0.0053 *
Gammarus nr. mucronatus	0.2	(0.13)	0.1	(0.03)					1.3	(0.53)	0.4	(0.13)	0.3	(0.19)	268	14.4	
Tubificidae	6.7	(1.25)	0.0	(0.00)					2.0	(0.51)	0.0	(0.00)	2.9	(0.73)	176	9.4	
Nematoda	2.1	(0.76)	0.0	(0.02)					3.3	(1.35)	0.0	(0.02)	0.7	(0.37)	119	6.4	
Chironomidae p,a	0.2	(0.13)	0.1	(0.03)					0.1	(0.08)	0.1	(0.04)	0.1	(0.07)	106	5.7	
Lepidoptera sp. X I	0.0	(0.00)	0.2	(0.04)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	93	5.0	
Baetidae	0.1	(0.07)	0.0	(0.01)					0.0	(0.00)	0.1	(0.06)	0.1	(0.13)	56	3.0	
Caenidae	0.1	(0.07)	0.0	(0.01)					0.1	(0.08)	0.1	(0.04)	0.0	(0.00)	53	2.8	
Ostracod sp. A	0.1	(0.07)	0.0	(0.00)					0.9	(0.47)	0.0	(0.02)	0.5	(0.08)	47	2.5	0.1593
Trichoptera sp. A I	0.0	(0.00)	0.0	(0.01)					0.0	(0.00)	0.0	(0.01)	0.0	(0.00)	36	1.9	
Hyalella azteca	0.0	(0.00)	0.1	(0.02)					0.0	(0.00)	0.0	(0.01)	0.0	(0.00)	33	1.8	
Coenagrionidae	0.1	(0.07)	0.0	(0.01)					0.1	(0.07)	0.0	(0.02)	0.0	(0.00)	32	1.7	
Ancylidae	0.1	(0.07)	0.0	(0.01)					0.0	(0.00)	0.0	(0.01)	0.0	(0.00)	16		
Ceratopogonidae p	0.0	(0.00)	0.0	(0.02)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	15		
Corixidae	0.0	(0.00)	0.0	(0.00)					0.2	(0.13)	0.0	(0.01)	0.1	(0.13)	13		
Lepidoptera sp. X p	0.0	(0.00)	0.0	(0.01)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	12		
Gastropoda sp. D	0.0	(0.00)	0.0	(0.01)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	12		
Littoridinops palustris	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	11		
Hydrellia sp. I	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	10		
Ceratopogonidae I	0.2	(0.13)	0.0	(0.00)					0.2	(0.13)	0.0	(0.00)	0.0	(0.00)	9		
Munna reynoldsi	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.01)	0.0	(0.00)	9		
Copepoda	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.01)	0.0	(0.00)	8		0.0892
Neretina usnea	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	6		
Gastropoda sp. C	0.1	(0.07)	0.0	(0.00)					0.0	(0.00)	0.0	(0.01)	0.0	(0.00)	6		
Rangia sp.	0.0	(0.00)	0.0	(0.00)					0.1	(0.08)	0.0	(0.01)	0.0	(0.00)	6		
Hydrellia sp. p	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	4		
Trichoptera sp. A p	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	3		
Trichoptera sp. B I	0.0	(0.00)	0.0	(0.00)					0.1	(0.07)	0.0	(0.00)	0.0	(0.00)	3		
Hymenoptera parasite	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	2		
Gastropoda sp. E	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	2		
Lepidoptera sp. A I	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	2		
Trichoptera sp. C I	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	2		
Trichoptera sp. C p	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	2		
Cladocera	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	2		
Ostracoda sp. B	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1		
Berosus sp.	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1		
Ant	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1		
Insect in Lep. sp. X p	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1		
Acarina	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1		
Fish egg	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1		
Insecta	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1		
Crustacea sp. A	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1		
Macrobrachium ohione	0.1	(0.07)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1		
Laeonereis culveri	0.0	(0.00)	0.0	(0.00)					0.1	(0.07)	0.0	(0.00)	0.0	(0.00)	1		
Saltricidae	0.0	(0.00)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.1	(0.07)	1		
Amphipoda sp. C	0.1	(0.07)	0.0	(0.00)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	1		
TOTAL ANIMALS	12.3	(1.37)	1.3	(0.13)					12.3	(1.44)	1.7	(0.25)	6.5	(1.09)	1866		0.0038 *

Figure 2.1a Average density (number / 20 cm^2) of total fauna (benthic plus epiphytic sample data normalized to number / 20 cm^2) and dominant prey species in October 1994. Similar letters indicate no significant difference between means.

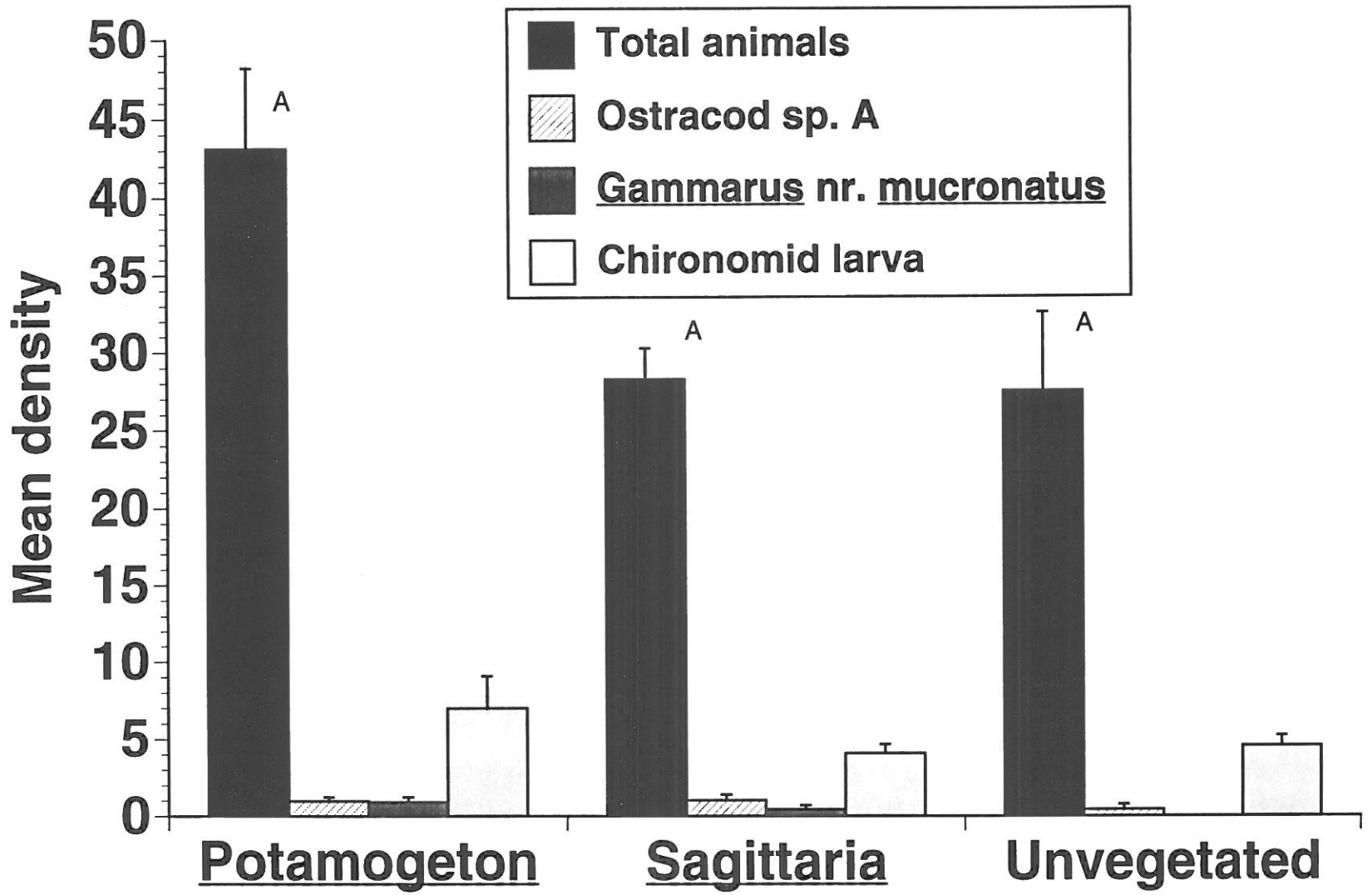
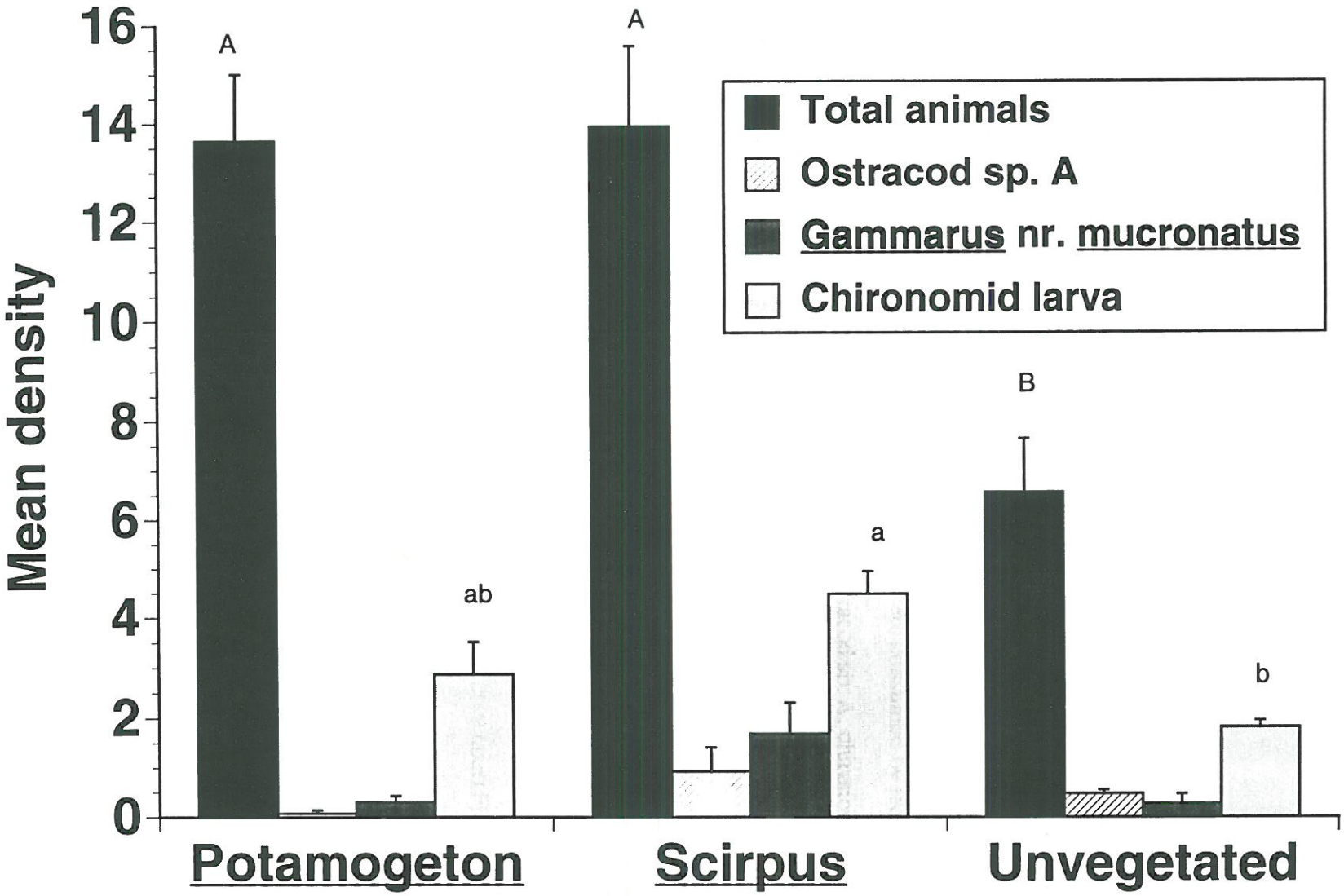

Total animals
Ostracod sp. A
Gammarus nr. mucronatus
Chironomid larva
Mean density
50
45
40
35
30
25
20
15
10
5
0
A
A
A
Potamogeton
Sagittaria
Unvegetated

Figure 2.1b Average density (number / 20 cm^2) of total fauna (benthic plus epiphytic sample data normalized to number / 20 cm^2) and dominant prey species in June 1995. Similar letters indicate no significant difference between means.


Mean density
16
14
12
10
8
6
4
2
0
A
A
B
ab
a
b
Total animals
Ostracod sp. A
Gammarus nr. mucronatus
Chironomid larva
Potamogeton
Scirpus
Unvegetated

Foraging experiments

Gut content

Seven taxa (4 crustaceans and 3 insects) were consumed by gulf killifish in my October experiments. Ostracod sp. A, Gammarus nr. mucronatus, and chironomid larva were numerically dominant in gulf killifish guts and accounted for >93% of the total number of prey organisms eaten (Table 2.3). Means of total volume, total number, and number of dominant prey taxa in gulf killifish guts were not significantly different among habitats (Fig 2.2a; Table 2.3).

Eight taxa (5 crustaceans, 2 insects, and nematodes) were consumed by freshwater gobies in the experiments conducted in June (Table 2.3). Ostracod sp. A, chironomid larva, and copepods were numerically dominant in freshwater goby guts and accounted for >93% of total prey organisms, most of which were ostracod sp. A (84%). Means of total volume, total number, and number of dominant prey taxa in freshwater goby guts were not significantly different among habitats (Fig. 2.2b; Table 2.3).

Prey selectivity

In October, gulf killifish showed some discrimination among prey taxa (Fig. 2.3a; Table 2.4). Gulf killifish showed an apparent preference for Ostracod sp. A and Gammarus nr. mucronatus over other prey species, but mean selection indices for these two taxa did not differ from each other. In contrast, mean selection indices for chironomid larva were all negative, implying that the larvae were either avoided by or largely inaccessible to fish. Mean selection indices of dominant prey taxa were not significantly different among habitats (Table 2.4).

Freshwater goby selected Ostracod sp. A over copepod, and both Ostracod sp. A and copepod were selected over chironomid larva in June (Fig. 2.3b; Table 2.4). Chironomid larvae mean selection indices were all negative as in October, indicating that they were avoided

Table 2.3 Mean density (number/gut) and mean volume (mm^3), with S.E. (one standard error), of prey taxa taken from guts of fish held in each habitat during October 1994 and June 1995. The total (number of animals collected in all habitats combined) is also listed. Each mean for a habitat was calculated from five replicate samples, and each of these habitat replicates was computed as the mean of three gut samples (three fish per cage). Results (P values) of ANOVA tests comparing means of prey number and volume of total animals and numerically dominant species among the three habitats are given. Relative abundance (RA) is given for those species with at least 1% relative abundance. Number of fish guts examined and number of empty guts found are listed for each habitat. Blank spaces represent month in which habitat was not sampled.

	Potamogeton nodosus				Sagittaria				Scirpus americanus				Unvegetated							
	Number		Volume		Number		Volume		Number		Volume		Number		Volume				P value	P value
Taxa	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Total	RA%	(number)	(volume)
October 1994 (gulf killifish)																				
Ostracoda sp. A	0.9	(0.69)	0.3	(0.28)	4.6	(2.80)	0.4	(0.26)					0.7	(0.59)	0.0	(0.02)	93	72.1	0.2283	0.4359
Gammarus nr. mucronatus	0.3	(0.16)	1.9	(1.36)	0.0	(0.00)	0.0	(0.00)					0.7	(0.30)	2.9	(1.45)	14	10.9	0.0925	0.2288
Chironomidae I	0.0	(0.00)	0.0	(0.00)	0.6	(0.32)	0.3	(0.20)					0.3	(0.19)	0.1	(0.13)	13	10.1	0.1911	0.4484
Corixidae	0.1	(0.08)	0.3	(0.26)	0.1	(0.08)	0.2	(0.13)					0.0	(0.00)	0.0	(0.00)	4	3.1		
Insecta sp.	0.0	(0.00)	0.0	(0.00)	0.1	(0.07)	0.1	(0.07)					0.1	(0.07)	0.0	(0.03)	2	1.6		
Chironomidae p	0.0	(0.00)	0.0	(0.00)	0.1	(0.07)	0.1	(0.07)					0.0	(0.00)	0.0	(0.00)	1			
Cladocera	0.0	(0.00)	0.0	(0.00)	0.1	(0.07)	0.1	(0.07)					0.0	(0.00)	0.0	(0.00)	1			
Copepoda	0.0	(0.00)	0.0	(0.00)	0.1	(0.07)	0.0	(0.01)					0.0	(0.00)	0.0	(0.00)	1			
Total volume			2.8	(1.88)			3.4	(1.58)							3.8	(2.06)	150.4			0.9259
Total number	1.3	(0.85)			5.6	(3.13)							1.7	(0.98)			129		0.2683	
Number of empty guts			9				8								8					
Number of guts			15				15								15					
June 1995 (freshwater goby)																				
ostracod spA	10.5	(3.46)	2.1	(0.57)					27.6	(8.41)	8.6	(2.93)	17.1	(2.07)	4.4	(0.64)	714	85.8	0.1181	0.0631
Chironomidae I	0.9	(0.78)	0.3	(0.30)					0.9	(0.26)	0.6	(0.36)	1.2	(0.50)	0.4	(0.18)	36	4.3	0.9170	0.6898
Copepoda	2.0	(2.00)	0.1	(0.08)					0.5	(0.39)	0.0	(0.01)	0.4	(0.19)	0.0	(0.01)	32	3.8	0.5904	0.6040
Nematoda	0.6	(0.37)	0.1	(0.09)					0.3	(0.13)	0.2	(0.13)	0.4	(0.40)	0.1	(0.05)	18	2.2		
Ostracoda sp. C	1.2	(1.20)	0.1	(0.08)					0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	0.0	(0.00)	12	1.4		
Gammarus nr. mucronatus	0.0	(0.00)	0.0	(0.00)					0.7	(0.38)	2.5	(1.41)	0.0	(0.00)	0.0	(0.00)	8	1.0		
Corixidae	0.0	(0.00)	0.0	(0.00)					0.1	(0.13)	0.1	(0.13)	0.5	(0.50)	0.7	(0.70)	7			
Chironomidae p	0.0	(0.00)	0.0	(0.00)					0.1	(0.10)	0.1	(0.10)	0.1	(0.08)	0.1	(0.07)	3			
Cladocera	0.0	(0.00)	0.0	(0.00)					0.2	(0.20)	0.0	(0.02)	0.0	(0.00)	0.0	(0.00)	2			
Total volume			11.1	(3.15)							15.1	(4.36)			17.0	(5.51)	410			0.6423
Total number	15.2	(7.26)							30.4	(8.76)			19.8	(2.04)			832		0.2894	
Number of empty guts			1								0				1					
Number of guts			11								13				14					

Figure 2.2a Average density (number / gut) and volume (mm^3) of prey per fish gut in October 1994. Means and standard errors (S.E.) were calculated from five samples. Error bars = 1 S.E..

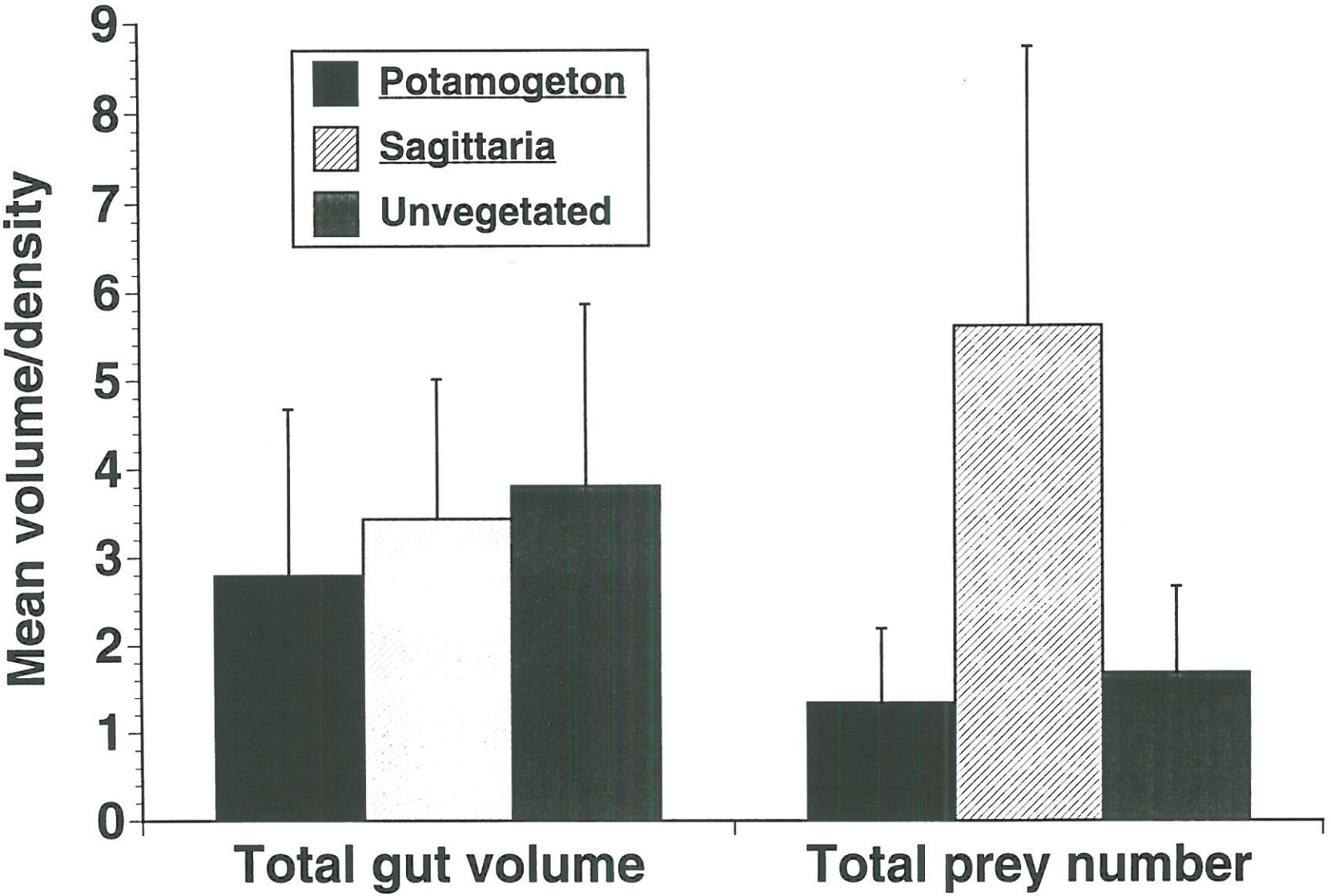

Mean volume/density
0
1
2
3
4
5
6
7
8
9
Potamogeton
Sagittaria
Unvegetated
Total gut volume
Total prey number

Figure 2.2b Average density (number / gut) and volume (mm^3) of prey per fish gut in June 1995. Means and standard errors (S.E.) were calculated from five samples. Error bars = 1 S.E..

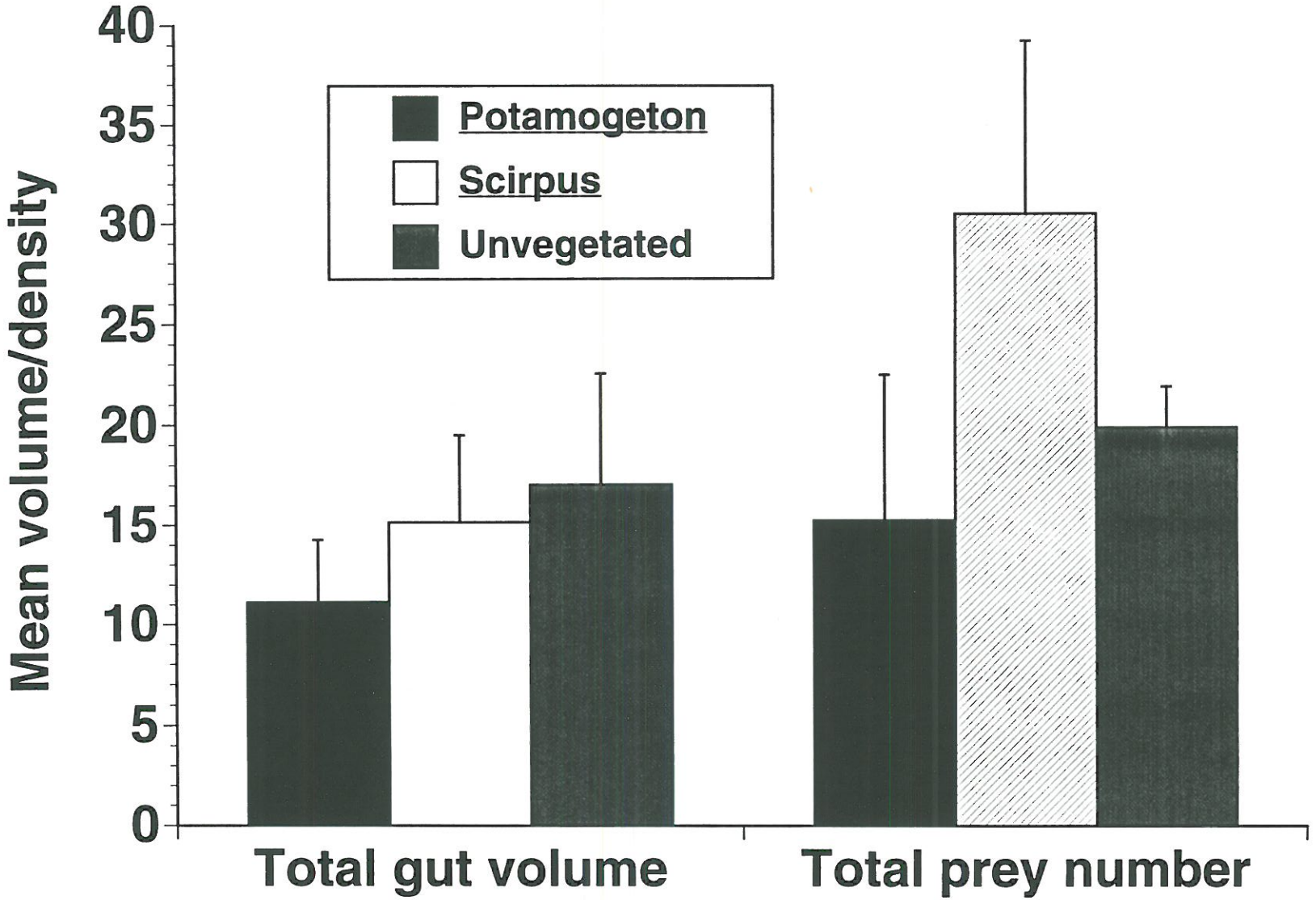

Mean volume/density
40
35
30
25
20
15
10
5
0
Potamogeton
Scirpus
Unvegetated
Total gut volume
Total prey number

Figure 2.3a Average selection indices of numerically dominant prey species for gulf killifish. Means and standard errors (S.E.) were calculated from five samples. Error bars = 1 S.E.. Similar letters indicate no significant difference between means.

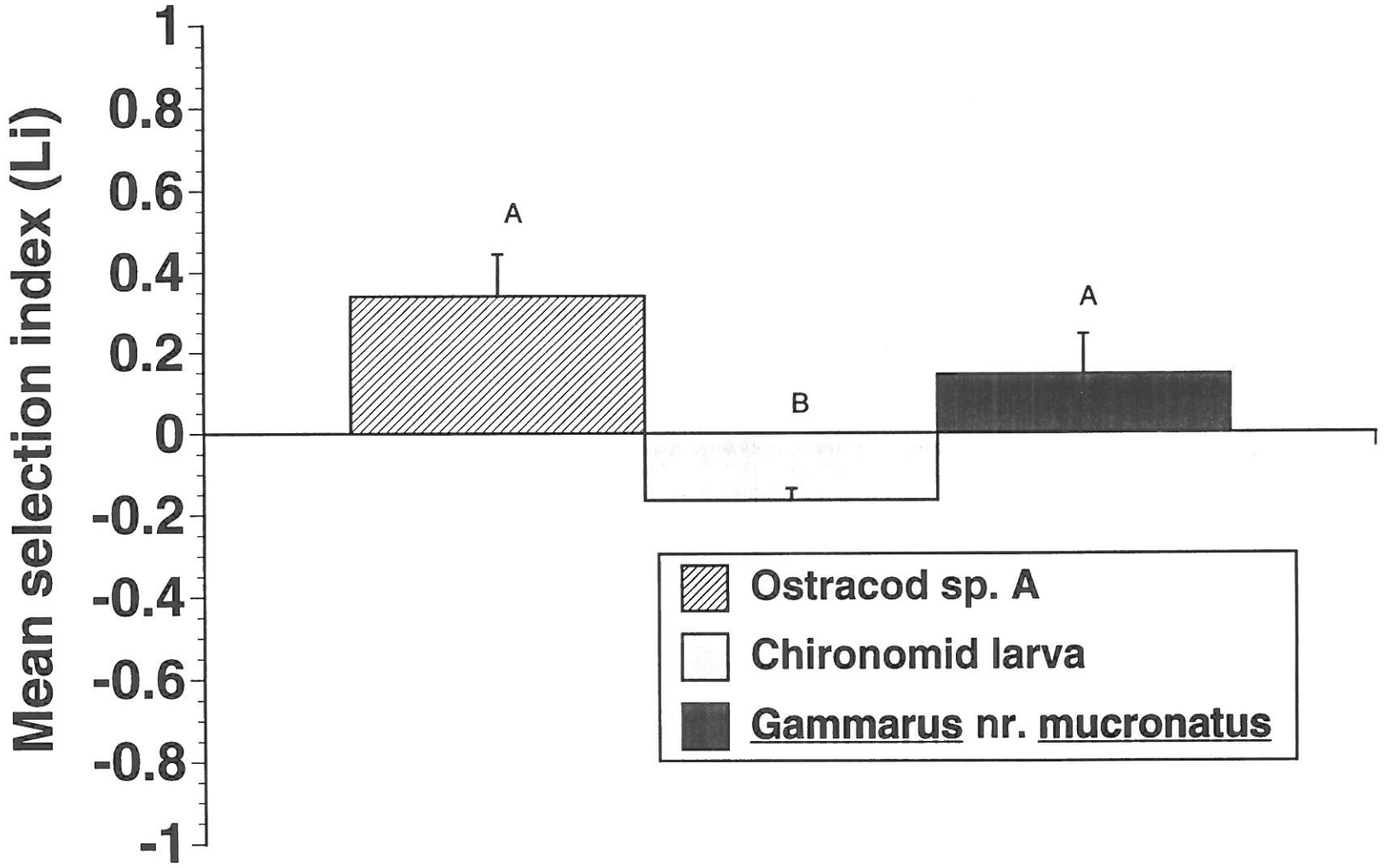
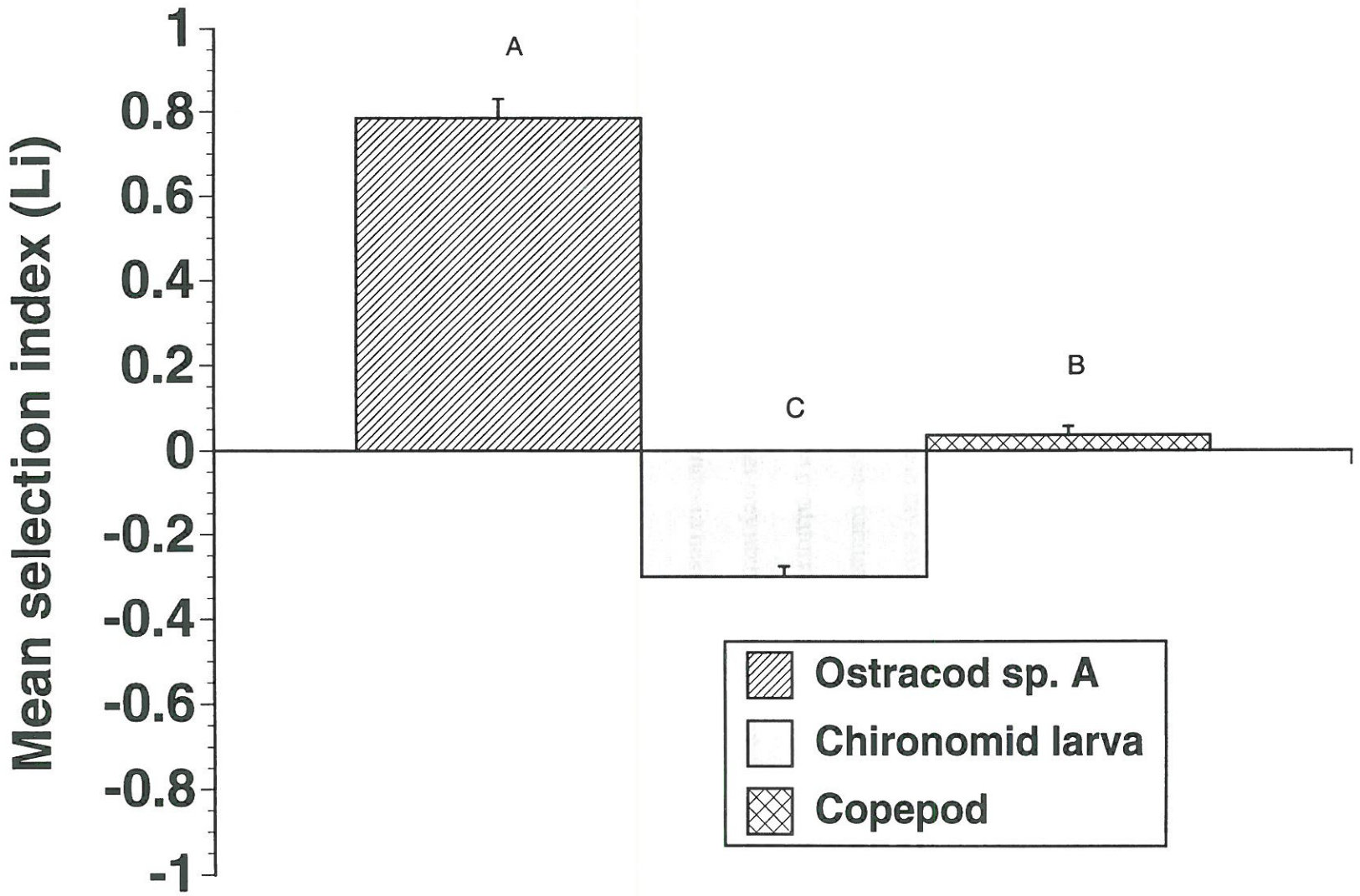

Mean selection index (Li)
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
A
B
A
Ostracod sp. A
Chironomid larva
Gammarus nr. mucronatus

Table 2.4 Mean selection indices (Li) and S.E. (one standard error) of prey species taken from guts of fish in each habitat. Each mean for a habitat was calculated from 5 replicate samples, and each of these habitat replicates was computed as the mean of three gut samples (three fish per cage). The mean selection index for important prey species for all habitats combined is also given. Results (P values) of ANOVA tests comparing mean selection indices of prey among the three habitats and among numerically dominant prey species also are given. Significant ANOVA is indicated by an (*). Blank spaces represent month in which habitat was not used in experiment.

	Potamogeton nodosus		Sagittaria		Scirpus americanus		Unvegetated		Among habitats	Mean sel. index		Among species	
Taxa	Mear	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	P value	of species	S.E.	P value	
October 1994 (gulf killifish)													
Ostracoda sp. A	0.46	(0.20)	0.44	(0.21)			0.13	(0.11)	0.3611	0.34	(0.10)		
Gammarus nr. mucronatus	0.13	(0.20)	-0.08	(0.03)			0.38	(0.20)	0.1727	0.14	(0.10)		
Corixidae	0.08	(0.07)	0.22	(0.20)			0.00	(0.00)	0.4371				
Cladocera	0.00	(0.00)	0.00	(0.00)			0.00	(0.00)	0.3966				
Copepoda	0.00	(0.00)	0.01	(0.00)			0.00	(0.00)	0.3966				
Chironomidae p	-0.01	(0.01)	0.18	(0.20)			0.00	(0.00)	0.4209				
Chironomidae l	-0.25	(0.06)	-0.14	(0.03)			-0.11	(0.04)	0.0882	-0.17	(0.03)		
												0.0006	*
June 1995 (freshwater goby)													
Ostracoda sp. A	0.83	(0.08)			0.75	(0.11)	0.78	(0.06)	0.8066	0.79	(0.05)		
Copepoda	0.05	(0.05)			0.04	(0.05)	0.02	(0.01)	0.8928	0.04	(0.02)		
Corixidae	0.00	(0.00)			0.03	(0.05)	0.01	(0.04)	0.8109				
Ostracoda sp. C	0.03	(0.03)			0.00	(0.00)	0.00	(0.00)	0.3966				
Cladocera	0.00	(0.00)			0.00	(0.01)	0.00	(0.00)	0.6610				
Nematoda	0.02	(0.04)			-0.05	(0.01)	-0.07	(0.05)	0.3236				
Chironomidae p	-0.06	(0.02)			-0.04	(0.01)	0.00	(0.01)	0.0183				
Gammarus nr. mucronatus	-0.06	(0.01)			-0.17	(0.05)	-0.05	(0.04)	0.0903				
Chironomidae l	-0.33	(0.02)			-0.33	(0.03)	-0.24	(0.06)	0.2470	-0.30	(0.02)		
												0.0001	*

Figure 2.3b Average selection indices of numerically dominant prey species for freshwater goby. Means and standard errors (S.E.) were calculated from five samples. Error bars = 1 S.E.. Similar letters indicate no significant difference between means.


Mean selection index (Li)
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
A
B
C
Ostracod sp. A
Chironomid larva
Copepod

or mostly inaccessible to fish. In June, mean selection indices for important prey taxa were not significantly different among habitats (Table 2.4).

DISCUSSION

No significant difference was found among habitats in either the volume or number of prey consumed by gulf killifish and freshwater goby. Except for chironomid larva, which was not a highly selected food, the estimates of natural distributions of the important prey taxa did not differ among habitats. Densities of total benthic and epiphytic fauna did differ significantly among habitats in June, but this was largely due to taxa that were not important or not highly selected as prey items by the predatory fish used in my experiments. Because natural distributions of important prey did not differ among habitats, perhaps it is not surprising that the number and volume of prey consumed by the predators in my experiments also did not differ among habitats. Had I found differences in prey abundance and prey consumed among habitats, this may have helped to explain differences in nekton habitat use I found in my Atchafalaya Delta study area (Chapter 1).

Although this was not the case in my study, adjacent estuarine habitats often differ substantially in prey availability. Banded killifish Fundulus diaphanus consumed more prey in vegetated than nearby unvegetated habitats in an Atlantic coast tidal freshwater marsh (Rozas and Odum 1988). In a Mississippi brackish marsh, gulf killifish diets were quantitatively and qualitatively different between fish that could forage only in subtidal areas and those that had access to the adjacent marsh surface (Rozas and LaSalle 1990). Fish that had the opportunity to feed on the marsh surface consumed more prey than those restricted to subtidal areas before the marsh flooded. Banded killifish in a Virginia tidal freshwater marsh consumed more food in enclosures on shallow-sloped depositional creek banks than in enclosures on nearby steep erosional banks (McIvor and Odum 1988).

Predators selectively feeding on prey associated with a particular habitat would be expected to preferentially use that habitat if other biotic and abiotic factors (e.g. presence or

absence of predators or conspecifics, salinity, temperature, water depth) are tolerable to the predator. Fish predators are often associated with habitats that contain their dominant prey species (Huh and Kitting 1985; Whitfield 1988). Higher abundances of predatory fishes were found in marshes adjacent to shallow, depositional creekbanks where foraging profitability had been shown to be higher than adjacent to steep erosional creekbanks (McIvor and Odum 1988). In an oligohaline estuary, small fish predators were more abundant in vegetated areas where small invertebrates, a major component of the fishes' diets, also occurred (Lubbers et al. 1990). These studies suggest that food availability may influence distributions of predatory fishes.

Both experimental fish species in my study utilized only a few of the potential prey taxa available. Although the composition of both fishes' diets was similar, their diets varied in the dominance of specific prey taxa. Amphipods and insects were consumed by gulf killifish in my study as documented in other studies of killifish diets (Harrington and Harrington 1961; Forman 1968; Ruebsamen 1972; Odum and Heald 1972; Subrahmanyam and Drake 1975; Perschbacher and Strawn 1986; Rozas and LaSalle 1990). In contrast to these other studies, however, polychaetes and crabs were not eaten by the fish in my study. Polychaetes are uncommon in tidal freshwater environments, and I rarely collected this taxon in my study area (1 in 75 samples); therefore, polychaetes were not available as prey. Although crabs were abundant in my study area, the fish used in the foraging experiments were relatively small (50-60 mm total length) and could potentially prey upon only very small juvenile crabs.

Copepods and nematodes were the third and fourth most abundant prey taxa, respectively, of freshwater goby in my study. However, these two taxa, along with polychaetes, were the most important prey of freshwater goby in a Louisiana oligohaline marsh (Fitzhugh and Fleeger 1985). Ostracod sp. A was much more important in freshwater goby diets in my study (86% relative abundance in guts) than ostracods were in Fitzhugh and Fleeger's (1985) study (2.2% relative abundance in guts). Curiously, chironomids were avoided by or were largely inaccessible to gobies in my study; yet, chironomids were the most

highly selected prey species in Fitzhugh and Fleeger's (1985) study. Perhaps the chironomids in my study are different species that are seldom eaten by freshwater goby, or the habitats in my study area provided a refuge for chironomids.

Artifacts are a potential problem in any experiment. Although I tried to avoid them, two potential artifacts could have confounded my results. In my study, a substantial portion of the gulf killifish (>50%) used in the foraging experiments had empty guts upon retrieval. This high percentage of empty guts may be construed by some as an artifact of the short time (3h) fish were allowed to feed or of reduced feeding caused by handling stress (although all animals appeared robust when released into enclosures). Freshwater gobies were allowed to feed for 40h in a similar experiment (Fitzhugh and Fleeger 1985). However, mummichogs Fundulus heteroclitus allowed to feed for only 2h in another study had adequate time to feed (Rozas and Odum 1988). The fishes I used in my experiments are estuarine residents adapted to cope with the limited feeding time available in some intertidal habitats and should have had adequate time to feed in a 3h period. A possible reason for lack of differences in food consumed and prey abundances among habitats is the proximity, and in some cases, intermixing of habitats. Unvegetated habitat was found in small patches interspersed among vegetated areas, and some marsh sites had small amounts of SAV (typically not P. nodosus) growing among the emergent macrophyte stems. Prey species normally restricted to a specific habitat could have moved between habitats used in the foraging experiments because of the close proximity or concurrence of habitats.

The natural distributions of most dominant prey species were not different among the habitats I sampled, nor was the foraging success of gulf killifish and freshwater goby different among habitats. Fishes selected only a few prey species from the large number available. Prey species of gulf killifish and freshwater goby were similar to prey eaten by these fish predators in other studies. Although other studies have shown a relationship between the distributions of predator and prey populations, my results do not support the hypothesis that the distribution of

fish predators (gulf killifish and freshwater goby) in my study area are influenced by the distribution of their prey.

SUMMARY

I quantified the nekton assemblages of submerged plant beds, marsh edge, and unvegetated bottom within the Atchafalaya Delta, a major tidal freshwater system of the northern Gulf of Mexico coast. In a comparison of habitat use by numerically dominant species, I found that there was little apparent habitat selection between SAV and marsh edge habitats. At least three factors may have contributed to this finding of no significant difference in the distributions of most species between SAV and marsh edge. Submerged plant beds and marsh edge habitats had similar substrate elevations and may have afforded equal protection from predators. In addition, SAV often occurred interspersed within marsh edge vegetation and thus increased the vegetation structural complexity of the marsh habitat. Consistent with much of the literature, vegetated habitats supported greater densities of nekton than unvegetated areas. Unlike most other studies that compared habitat use between SAV and unvegetated bottom, substrate elevation was not confounded with habitat type in my study. Because substrate elevations in SAV and unvegetated habitats were not significantly different, water depth is unlikely to have influenced nekton distributions between these habitats. Nekton apparently selected vegetated backmarsh habitats over streamside marsh; the greater use of backmarsh habitats may be due to a lack of shallow SAV adjacent to streamside marsh. The high densities of juvenile blue crab in vegetated habitats indicate that vegetated, tidal freshwater habitats of the Atchafalaya River Delta may provide an important nursery function for this species. Foraging experiments showed that common fish predators did not consume prey differentially among habitats. This result may have been due to the similarity in prey abundances and prey availability among habitats that I documented. Although nekton species apparently select some habitats over others (principally vegetated habitats over unvegetated bottom), my study indicates that factors other than prey availability may influence patterns of nekton distribution among habitats.

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ABSTRACT

I sampled nekton (fishes and crustaceans) in submerged aquatic vegetation (SAV) (Potamogeton nodosus, Najas guadalupensis), marsh (Sagittaria spp, and Scirpus americanus), and unvegetated bottom associated with islands in the Atchafalaya River Delta, Louisiana. The purpose of my study was to quantify nekton densities in these major aquatic habitats and to document the relative importance of habitats to numerically dominant aquatic organisms. I collected a total of 33 species of fishes and 7 species of crustaceans in 298 1 m^2 throw trap samples taken over three seasons: summer (July and August 1994), fall (September and October 1994), and spring (May and June 1995). Fishes accounted for >65% of the total organisms I collected. Vegetated habitats generally supported much higher nekton densities than unvegetated sites, although bay anchovies Anchoa mitchilli was more abundant over unvegetated bottom than in most vegetated habitats. Within vegetated habitats, most species showed no apparent preference between SAV and marsh. However, inland silversides Menidia beryllina and freshwater gobies Gobionellus shufeldti were most abundant in Scirpus marsh in summer, and blue crabs Callinectes sapidus were most abundant in SAV (Potamogeton) in spring. Several species (sheepshead minnow Cyprinodon variegatus, rainwater killifish Lucania parva, and blue crab) apparently selected vegetated backmarsh habitat over streamside Scirpus marsh. Freshwater gobies, in contrast, were most abundant in streamside Scirpus marsh. Densities of juvenile blue crabs were high (up to 17 m^{-2}) in vegetated delta habitats and comparable to values reported from more saline regions of Gulf coast estuaries. Shallow vegetated habitats of the Atchafalaya Delta and other tidal freshwater systems of the Gulf coast may be important nursery areas for blue crabs and other estuarine species. In addition to sampling major nekton habitats, I used two predatory fishes (gulf killifish Fundulus grandis in October and freshwater goby in June) in foraging experiments to estimate the relative foraging profitability among habitats and the influence of prey availability on nekton distributions in my study area. I placed fish in enclosures containing submerged

aquatic vegetation (Potamogeton nodosus), marsh (Scirpus americanus), and on unvegetated bottom and allowed them to forage for approximately 3 hr. At the conclusion of experiments, I collected the fish from the cages and examined their gut contents. I enumerated and identified the gut contents to the lowest taxon possible. In addition to foraging experiments, I took benthic core and epiphytic quadrat samples to estimate the standing crops of potential invertebrate prey. I compared the mean number and volume of prey contained in fish guts, and the mean densities of invertebrate prey taken in benthic and epiphytic samples, among habitats. Using the relative abundances of prey taxa collected from guts and habitats, I determined feeding preferences of fish predators among both habitats and prey taxa using the linear index of food selection (Strauss 1979). Nine taxa, numerically dominated by ostracod sp. A, were consumed by gulf killifish and freshwater gobies. Ostracod sp. A was highly selected by both experimental fish predators, whereas chironomid larva, another abundant prey taxon, was either avoided or unavailable. Means of total volume, total number, and dominant prey number consumed by gulf killifish and freshwater gobies were not significantly different among habitats; this result may be attributed to the fact that densities of prey were not different among habitats. The results of my study do not support the hypothesis that the distribution of nekton in my study area was influenced by prey distributions and prey availability (at least for gulf killifish in October and freshwater gobies in June).

BIOGRAPHICAL SKETCH

David Castellanos was born 3 April 1968 in New Orleans, Louisiana. He graduated from Brother Martin High School in 1986. Following high school, David attended the University of New Orleans and earned a B.A. in Biological Sciences (Chemistry minor) in 1991. David is currently a candidate for a Master of Science degree in Biology at the University of Southwestern Louisiana.